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Analyse mathématique et numérique de modèles de propagation en épidémiologie évolutive

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À Papi Fred.
« Je suis un homme,
donc un lutteur »

Chapitre 1

Introduction

Cette thèse porte sur l'étude mathématique de modèles de biologie théorique, principalement issus de l'épidémiologie évolutive. Elle s'inscrit dans une longue tradition d'échanges entre les deux disciplines qui — bien que souvent moins visibles pour un observateur extérieur que ceux s'effectuant entre, par exemple, les mathématiques et les sciences physiques — a engendré une littérature importante et une culture spécifique. Avant de présenter les résultats de mes travaux, je souhaite exposer brièvement quelques modèles (et les concepts et notations indispensables à leur compréhension), ainsi que quelques événements historiques marquants.

1.1 Motivations et contexte biologique

1.1.1 Principes généraux

La naissance de la biologie en temps que science est souvent attribuée à Darwin, avec son ouvrage *De l'origine des espèces* (1859). Néanmoins, il faut signaler que Darwin s'intègre lui aussi dans une histoire de la réflexion sur le vivant en temps qu'objet d'étude rationnelle. Ainsi, Descartes, par exemple, bien qu'il ne s'intéresse pas à la diversité des espèces, propose dans le *Discours de la méthode* (1637) un modèle mécanistique pour expliquer le fonctionnement des animaux (animal-machine) ; Maupertuis, dans *La Vénus Physique* (1745), introduit des idées modernes sur l'hérédité et peut être considéré comme un autre précurseur des théories de l'évolution ; citons également Lamarck, qui a lui aussi présenté une théorie de l'évolution basée sur l'hérédité des caractères acquis (la fonction crée l'organe) — désormais invalidée par la biologie moléculaire, même si la mise en évidence des mécanismes épigénétiques bouleverse certains dogmes de l'hérédité mendélienne [68]. Ce dernier est également l'un des premiers à avoir considéré l'étude des êtres vivants commme une discipline à part entière, séparée de la physique et chimie ; il est aussi un précurseur dans l'utilisation du terme *biologie*. Darwin est sans doute présenté aujourd'hui comme le père de la théorie moderne de l'évolution du fait de la controverse qui suivit la publication de *De l'origine des espèces* : son caractère blasphématoire a permis un renversement des dogmes qui accompagnaient jusqu'alors la réflexion sur le vivant.

Darwin propose un modèle explicatif pour la diversité des espèces et des caractères (*phénotypes*) observés dans le monde animal. Il base sa réflexion sur trois grands principes : un principe de *variation*, un principe d'*hérédité* et un principe de *sélection*. Par principe de variation nous entendons qu'au sein d'une population d'individus susceptibles de se reproduire, tous ne présentent pas des caractères *identiques*, mais seulement des caractères *similaires* : ainsi une girafe (pour reprendre un exemple classique) peut présenter un cou plus ou moins long, un chien un caractère plus ou moins sociable, etc. Le principe d'hérédité stipule que les caractères des descendants ressembleront à ceux des parents. Rappelons que l'ADN, qui donnera un support physique à cette hérédité, n'est pas encore découvert à cette époque. Ainsi des girafes au grand cou auront probablement des girafons dotés eux aussi d'un grand cou, bien que non systématiquement. Enfin, au fil des générations, certains caractères donnent un avantage aux individus qui les possèdent et leur permettent de se reproduire mieux que les autres, ce qui rend ces caractères plus présents dans la population : c'est le principe de sélection, parfois appelé *sélection naturelle*. Ainsi des girafes au grand cou pourront mieux se nourrir que les autres car elles auront accès à plus de nourriture. Darwin note avec nous que, bien que ces principes n'aient jamais été formulés auparavant, ils ont été largement utilisés au cours du temps par les éleveurs qui, par une sélection *artificielle* des caractères, ont produit des races d'élevage adaptées aux besoins de l'homme : vache à viande, chien de chasse, etc. Cette même sélection explique également que, si une population est soumise à des contraintes naturelles variées, elle peut se scinder en deux sous-populations qui se distancent au point de ne plus pouvoir se reproduire entre elles, créant deux espèces séparées.

Ces trois principes sont toujours d'actualité et d'ailleurs repris dans la plupart des modèles théoriques en biologie, que se soit en dynamique des populations, génétique des populations, dynamique adaptative, génétique quantitative...

1.1.2 Épidémiologie et évolution

Dynamique épidémiologique

Dans la suite nous nous intéressons à une classe particulière d'espèces, principalement constituée des agents causeurs de maladies infectieuses : bactéries, virus, i.e. les formes de vies dont le milieu principal est un individu d'une autre espèce. L'étude de la variation temporelle des densités de populations infectées par un ou plusieurs parasites porte le nom d'*épidémiologie*.

Il semble que les premiers modèles d'épidémiologie moderne aient été introduits il y a une centaine d'années par Ross [180], Ross et Hudson [181, 182], et plus tard Kermack et McKendrick [137] (leur étude se poursuivant dans les années suivantes [138, 139]). Rappelons néanmoins que, dès 1760, Daniel Bernouilli [32] publia une étude statistique de l'épidémie de petite vérole, visant à déterminer le gain en espérance de vie en fonction des politiques publiques d'inoculation de formes faibles de la maladie. Cette étude a été reprise *a posteriori* par Dietz et Heesterbeek [75].

Dérivons maintenant un modèle très simple d'épidémiologie, que nous nommerons *modèle de Kermack-McKendrick* en référence au modèle plus complexe discuté dans [137] (et repris en détail dans [188]). Nous considérons une population théorique d'hôtes qui se trouvent dans un état *susceptible* (S) ou *infecté* (I). Désignons respectivement par $S(t)$ et $I(t)$ le nombre d'hôtes susceptibles et infectés. Dans un intervalle de temps infinitésimal $(t, t+dt)$, nous pouvons établir le bilan des nouvelles infections et des guérisons :

$$\begin{cases} S(t+dt) - S(t) = -\beta S I dt \\ I(t+dt) - I(t) = \beta S I dt - \gamma I dt. \end{cases}$$

Dans ce calcul, nous avons utilisé un certain nombre d'hypothèses sous-jacentes. Premièrement, nous négligeons la dynamique intrinsèque de la population d'hôtes : il n'y a pas de mort naturelle, ni de naissance, entre les instants t et $t+dt$. Ensuite, les événements susceptibles de modifier la population suivent une loi exponentielle : les rencontres entre deux hôtes suivent une loi exponentielle de taux 1, et lors d'une rencontre entre un hôte sain et un hôte infecté, l'infection se transmet avec une probabilité β, ce qui se traduit par le terme d'échange $\pm\beta S I dt$. Finalement, l'infection est soit fatale soit parfaitement immunisante, les effets de l'immunité et de la mortalités étant pris en compte dans le paramètre γ. Ce modèle peut être résumé par le schéma :

$$S \xrightarrow{\beta I} I \xrightarrow{\gamma}$$

où les nœuds représentent les états des hôtes, les flèches les transitions entre états et leurs étiquettes les taux auxquels les transitions interviennent. La flèche sortante correspond à un terme de perte.

En prenant la limite $dt \to 0$, nous obtenons un système d'équations différentielles qui décrit la dynamique de l'infection :

$$\begin{cases} \frac{dS}{dt} = -\beta S I \\ \frac{dI}{dt} = \beta S I - \gamma I. \end{cases} \tag{1.1}$$

Partant d'une quantité initiale $S(t=0) = S_0$ et $I(t=0) = I_0$, nous pouvons alors reconstruire la population susceptible $S(t)$ et la population infectée $I(t)$ à tout temps $t > 0$.

Remarquons que la quantité $R_0 := \frac{\beta S_0}{\gamma}$ détermine la dynamique qualitative de l'équation (1.1). En effet, si $R_0 < 1$, la population infectée I est initialement décroissante ($\frac{dI}{dt} < 0$) et elle le reste en temps $t > 0$: l'épidémie ne se propage pas dans la population. En revanche si $R_0 > 1$, la population infectée connaît initialement une phase de croissance ($\frac{dI}{dt} > 0$) avant de s'éteindre. Intuitivement, R_0 correspond au nombre moyen d'infections générées par un unique individu infecté dans une population naïve ; d'où son appellation de *taux de reproduction de base*. Nous retrouvons, dans la dynamique de l'équation (1.1) comme dans l'intuition, le fait que R_0 détermine le sort de l'infection à long terme : pour que l'épidémie se propage dans la population, il *faut* que $R_0 > 1$.

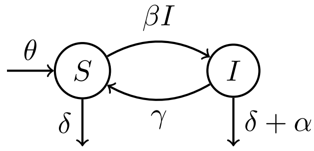
La quantité R_0 est un paramètre clé en épidémiologie, fréquemment utilisé pour prévoir, par exemple, le potentiel invasif d'un nouveau pathogène ; il possède de nombreuses généralisations à des modèles plus complexes (voir par exemple [74]). Pour une description plus précise des interactions entre mathématiques et épidémiologie, nous renvoyons à [73].

Bien qu'excessivement simple, le modèle (1.1) a été utilisé en pratique dans [137] pour reconstituer *a posteriori* une épidémie de peste dans l'île de Bombay entre le 17 décembre 1905 et le 21 juillet 1906, avec une précision remarquable ; [188] évoque d'autres applications très pratiques, comme la prévision du nombre de personnes à vacciner pour empêcher la propagation d'une épidémie, avec des conséquences très pragmatiques comme le coût prévisionnel de la campagne de vaccination. D'autre part, les quantités β, γ et R_0 sont fréquemment estimées lors d'études de terrain [73, 10].

La simplicité du modèle (1.1), pourtant, ne nous permet pas de pousser plus loin l'analyse théorique et en particulier d'appliquer la théorie darwinienne. En effet, il prédit l'extinction du parasite en temps long et un unique équilibre $I = 0$ et $S = \frac{\gamma}{\beta}$.

Une application de la théorie de l'évolution darwinienne

Pour rendre compte de dynamiques sans extinction du pathogène, introduisons maintenant un modèle plus complexe. Nous prenons en compte une *dynamique d'immigration* et de *mortalité* sur la population d'hôte, et ajoutons une charge de mortalité additionnelle sur la population d'infectés. Cela induit un modèle légèrement plus complexe que nous pouvons résumer par le schéma :



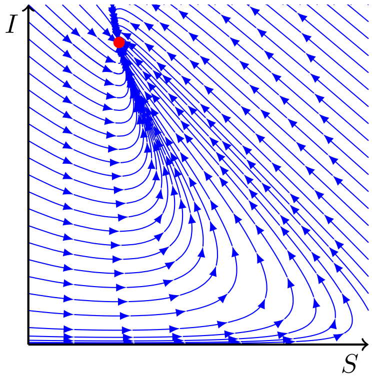


FIGURE 1.1 – Plan de phase associé au système (1.2)

et qui se traduit par le système d'équations différentielles :

$$\begin{cases} \frac{dS}{dt} = \theta - \delta S - \beta SI + \gamma I \\ \frac{dI}{dt} = \beta SI - (\delta + \alpha)I - \gamma I. \end{cases} \tag{1.2}$$

Ici, θ est le paramètre d'immigration des hôtes, assimilé à un terme source constant ; δ est la mortalité naturelle des hôtes, α est le surcoût de mortalité induit par l'infection ; enfin β est le paramètre de transmission et γ le paramètre de guérison. Nous négligeons ici l'immunité des hôtes guéris.

Nous avons alors $R_0 = \frac{\beta S}{\delta+\alpha+\gamma}$, et R_0 détermine la dynamique en temps long du système :

- si $R_0 < 1$, on a un unique équilibre stable $(\bar{S}, \bar{I}) := (\frac{\theta}{\delta}, 0)$, i.e. le pathogène ne persiste pas dans la population d'hôtes ;

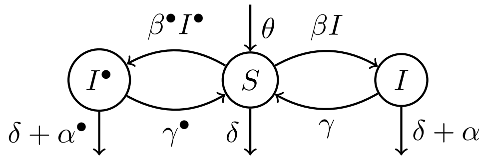
- si $R_0 > 1$, l'équilibre $(\bar{S}, \bar{I}) = (\frac{\theta}{\delta}, 0)$ devient instable et on a un unique équilibre globalement stable $(S_e, I_e) := (\frac{\delta+\alpha+\gamma}{\beta}, \frac{\beta\theta-\delta(\delta+\alpha+\gamma)}{\beta(\delta+\alpha)})$; il y a coexistence des hôtes et des parasites en temps long (voir le plan de phase en Figure 1.1).

La dynamique de ce système a été étudiée en détails dans [142, 131].

Le cas où $R_0 > 1$ est particulièrement intéressant car il y a persistence en temps long du pathogène. Cela permet de poser la question de l'*évolution* du pathogène, i.e. des *changements en trait* inévitables dans une population. Cette question tombe dans le cadre de la théorie de l'évolution introduite en section 1.1.1.

Une première réponse peut être avancée par la théorie de la *dynamique adaptative* [105, 104] sous l'hypothèse que les mutations sont rares.

Dans notre contexte simplifié, le *phénotype* des pathogènes est entièrement caractérisé par les nombres réels β, α et γ. Pour déterminer comment l'évolution va modifier les traits du pathogène, envisageons une situation d'équilibre (S_e, I_e) où le pathogène possède le phénotype (β, α, γ) et introduisons dans le système un mutant initialement rare $I^\bullet$ ayant pour phénotype $(\beta^\bullet, \alpha^\bullet, \gamma^\bullet)$. Le cycle de vie devient plus complexe :



et l'évolution du système se traduit par :

$$\begin{cases} \frac{dS}{dt} = \theta - \delta S - \beta SI - \beta^\bullet SI^\bullet + \gamma I + \gamma^\bullet I^\bullet \\ \frac{dI}{dt} = \beta SI - (\delta + \alpha)I - \gamma I \\ \frac{dI^\bullet}{dt} = \beta^\bullet SI^\bullet - (\delta + \alpha^\bullet)I^\bullet - \gamma^\bullet I^\bullet, \end{cases} \tag{1.3}$$

avec les conditions initiales $(S, I, I^\bullet)(t = 0) = (S_e, I_e, I_0^\bullet)$ où $I_0^\bullet \ll 1$. Intéressons nous à la stabilité exponentielle de l'état stationnaire $(S_e, I_e, 0)$. On constate que la matrice jacobienne

$$Jac(S_e, I_e, 0) = \begin{pmatrix} \frac{\gamma - \beta\theta}{\alpha + \gamma} & -(\alpha + \delta) & \gamma^\bullet - \frac{\beta^\bullet}{\beta}(\delta + \alpha + \gamma) \\ \frac{\beta\theta - \delta(\delta + \alpha + \gamma)}{\delta + \alpha} & 0 & 0 \\ 0 & 0 & (\delta + \alpha^\bullet + \gamma^\bullet)(R_m^\bullet - 1) \end{pmatrix}$$

a comme valeur propre $(R_m^\bullet - 1)(\delta + \alpha^\bullet + \gamma^\bullet) > 0$, où $R_m^\bullet := \frac{\beta^\bullet S_e}{\delta + \alpha^\bullet + \gamma^\bullet}$ ce qui montre que l'équilibre est instable si $R_m^\bullet > 1$. Dans ce cas, le mutant peut envahir la population.

Nous devons maintenant déterminer si le mutant remplace effectivement le pathogène en place. L'équilibre $(\bar{S}, 0, 0)$ est instable, et l'équilibre où seul le mutant est présent, $(S_e^\bullet, 0, I_e^\bullet) := (\frac{\delta + \alpha^\bullet + \gamma^\bullet}{\beta^\bullet}, 0, \frac{\beta^\bullet \theta - \delta(\delta + \alpha^\bullet + \gamma^\bullet)}{\beta^\bullet(\delta + \alpha^\bullet)})$, est localement stable. Nous ne pouvons pas exclure a priori l'existence de dynamiques plus complexes sans un travail plus approfondi ; notons toutefois qu'il existe des conditions sur les coefficients — détaillées dans [14] sous un formalisme un peu différent — sous lesquelles on peut effectivement prouver que le mutant remplace le pathogène résident, et d'autres sous lesquelles les parasites coexistent.

Ici, l'analyse locale montre que le taux de reproduction de base du mutant $R_0^\bullet$ doit être plus grand que R_0 pour que le mutant puisse persister dans la population. Cela correspond à un fait bien établi dans les modèles simples de dynamique adaptative : l'évolution tend à augmenter le taux de reproduction de base [152]. Des dynamiques plus complexes peuvent toutefois perturber ces prédictions, comme la prise en compte des infections multiples.

D'autre méthodes sont néanmoins nécessaires pour déterminer l'issue à court terme d'une épidémie, lors par exemple de l'émergence d'une nouvelle souche virale ou bactérienne. La dynamique adaptative ne peut, par essence, répondre à ce genre de questions qui portent sur des régimes transitoires. Citons par exemple des méthodes issues de la génétique des populations et de la génétique quantitative discutées notamment dans [72, 70, 56], qui s'appuient sur l'équation de Price [170], et qui peuvent traiter ce genre de questions. Ces méthodes permettent de suivre les caractéristiques statistiques de la population au cours du temps en fonction des covariances entre les traits observés et la *fitness* associée à ces traits. Elles donnent accès à l'étude de l'évolution en temps court d'une population, et peuvent réconcilier les dynamiques épidémiologiques et évolutives des populations d'hôtes et de parasites.

1.1.3 Structure spatiale et propagation

Nous avons établi les modèles présentés en section 1.1.2 sous l'hypothèse initiale d'une population bien mélangée, où tous les hôtes se rencontrent au hasard. Cette hypothèse présente l'avantage de simplifier les dynamiques épidémiologiques et évolutives et de donner une première vision des forces qui s'exercent sur les populations ; les modèles se réduisent à des systèmes d'équations différentielles ordinaires dont l'étude, bien qu'elle puisse être extrêmenent complexe, possède une littérature très ancienne et développée en mathématiques. Toutefois cette hypothèse reste limitante pour l'analyse de certaines questions, notamment relatives à la propagation spatiale des pathogènes, et n'est pas toujours biologiquement justifiée.

Si nous voulons étudier le comportement spatial d'une épidémie, il est nécessaire de postuler une *structure* dans la population d'hôtes. Ces structures sont naturellement représentées par des graphes (ou réseaux) d'interaction, et dans une certaine limite engendrent des modèles intégro-différentiels ou de réaction-diffusion-transport.

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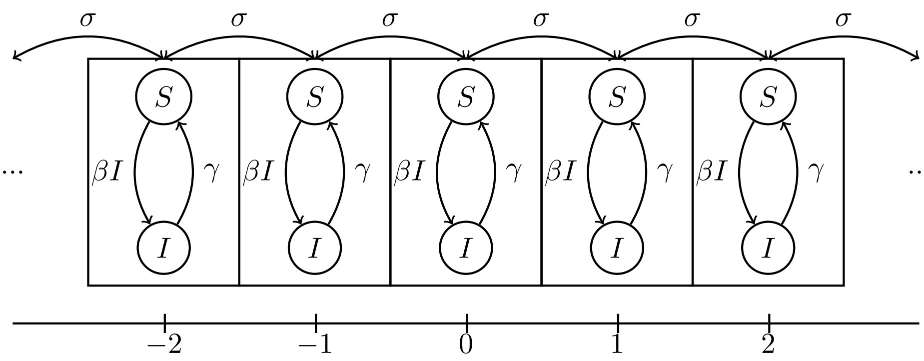
Nous présentons ici un premier modèle possédant une structure spatiale simple mais qui permet déjà de répondre (dans un champ d'applications limité) à la question de la propagation spatiale d'une épidémie. Nous considérons ici une structure *linéaire* : des sites sont placés sur une droite, à l'intérieur desquels les hôtes se rencontrent au hasard, comme dans la section 1.1.2. Nous supposons de plus que deux sites voisins échangent des individus au hasard en conservant un nombre d'individus par site constant. Nous envisageons un pathogène ayant des caractéristiques similaires à celui du modèle (1.1), mais pour lequel l'infection n'est ni immunisante ni fatale. Enfin, nous supposons que l'infection n'a pas d'impact sur le déplacement des hôtes. Ce modèle peut être représenté comme suit :



et dans une certaine limite d'échelle détaillée dans [115], nous obtenons le modèle de réaction-diffusion :

$$\begin{cases} \frac{\partial S}{\partial t} = \sigma \frac{\partial^2 S}{\partial x^2} - \beta S I + \gamma I \\ \frac{\partial I}{\partial t} = \sigma \frac{\partial^2 I}{\partial x^2} + \beta S I - \gamma I \end{cases}$$

où la variable d'espace x représente la structure spatiale. Un modèle légèrement différent a été utilisé par Noble [159] en 1974 pour reconstituer l'épidémie de peste noire du XIV$^{\text{e}}$ siècle, et repris en exemple dans [188].

Avec nos hypothèses, nous pouvons simplifier l'équation en remarquant que $\partial_t(S+I) - \sigma\partial_x^2(S+I) = 0$: la population totale $I+S = N$ est constante. Nous pouvons alors réécrire le système et établir une équation autonome sur la densité d'hôtes infectés :

$$\partial_t I - \sigma \frac{\partial^2 I}{\partial x^2} = I(\beta(N-I) - \gamma) = (\beta N - \gamma) I \left(1 - \frac{I}{N - \frac{\gamma}{\beta}}\right). \tag{1.4}$$

Nous retrouvons une équation très classique — dont nous analyserons la dynamique un peu plus en détail en section 1.2.1 —, qui prévoit une propagation à vitesse constante et donne une formule explicite de la vitesse :

$$c := 2\sqrt{\sigma(\beta N - \gamma)}.$$

Historiquement, l'équation (1.4) a été introduite en 1937 par Fisher [89] et simultanément par Kolmogorov, Petrovskii et Piskunov [141] dans le domaine de la génétique des populations, pour étudier la vitesse de propagation d'un allèle bénéfique dans une population structurée en espace. D'autres modèles utilisent le même formalisme dans des contextes très différents : par exemple, Skellam [190] (1951) utilise un modèle semblable pour une population de rats musqués en Europe centrale.

Le modèle (1.4) appartient à la grande famille des modèles de réaction-diffusion. Ces modèles sont précieux car ils permettent de reconstruire ou prévoir l'étendue spatiale d'une épidémie, notamment par le biais des *fronts de propagation* ou *fronts progressifs* associés (en anglais : *traveling waves*).

Notons que ces modèles diffusifs ne sont évidemment pas universels : ils sont par exemple discutés dans [143], où sont proposés d'autres modes de dispersion en meilleure adéquation avec certains relevés de terrain. Il reste que les modèles de réaction-diffusion on été largement étudiés par le passé et continuent à l'être, et constituent par la richesse des outils mathématiques à disposition un outil fondamental en modélisation.

Enfin, d'autres questions que celles des invasions peuvent être abordées grâce à des modèles structurés en espace : par exemple, la répartition à l'équilibre endémique de pathogènes dans des populations d'hôtes inhomogènes. Ces questions peuvent être traitées dans des modèles en espace continu ou dans des réseaux discrets *ad hoc*, comme par exemple dans [185, 154].

Dynamique adaptative et épidémiologie évolutive

Les techniques de dynamique adaptative peuvent être appliquées dans les modèles de *lattice* (i.e. dans des espaces discrets de type réseau), sans que la formulation de la théorie ne change radicalement [41, 58, 175, 148]. Les conclusions, en revanche, sont en général quantitativement différentes de celles du cas bien mélangé, le mutant introduit ayant à envahir d'une part la population voisine de son lieu d'introduction, puis la population à échelle globale. Par exemple, dans [41], les auteurs prédisent que le phénotype évolutivement stable (ESS, pour *Evolutionary Stable State*) dans une population où les infections ont lieu localement, a une virulence moins grande que celle de l'ESS dans une population bien mélangée. Dans une étude plus récente [213], les auteurs discutent de l'influence de la structure spatiale sur l'évolution d'un parasite dans une population d'hôtes partiellement vaccinée.

L'étude de l'évolution en régime transitoire a reçu beaucoup d'attention ces dernières années, particulièrement dans des thématiques d'écologie évolutive et d'invasion biologique. Encore une fois l'objectif peut être soit de préciser des résultats existants en prenant en compte l'influence de la structure spatiale, soit d'étudier des quantités inaccessibles à la théorie en milieu bien mélangé (comme l'aire de répartition). Hallatschek *et al*, par exemple, ont étudié expérimentalement [117] puis théoriquement [118, 119] des problématiques de *gene surfing* pour les populations en expansion, i.e. le rôle particulier de la dérive génétique (*genetic drift*) lors d'invasions et son influence sur la composition génétique de la population ultérieurement établie. Ils argumentent en particulier que sous certaines conditions portant sur la dynamique d'invasion, des mutations neutres voire délétères peuvent se retrouver sur-représentées dans la population par le simple fait qu'elles soient portées par les individus pionniers (*effet fondateur* ou *founder effect*). Garnier, Giletti, Hamel et Roques [102] envisagent différentes dynamiques de propagation déterministes et leurs conséquences sur le maintien ou la déplétion de la diversité génétique. Perkins [164] analyse différents types d'interactions entre espèces invasive et résidente dont l'une est évolutivement instable. D'autres questions en écologie évolutive nécessitent par essence une structure spatiale, comme l'évolution de la dispersion [177]. Perkins, Philips *et al* [165] recensent un phénomène d'accélération d'invasion lié à l'évolution des pattes des crapauds buffles en Australie et à un phénomène de *tri en espace* [189]. A ce sujet un modèle mathématique a été développé et analysé dans [43, 42]. De son côté, Phillips [166] a étudié l'impact d'une variabilité dans le taux de croissance des individus sur la propagation spatiale. Signalons enfin [2] où les auteurs analysent un modèle mathématique donnant des conditions sur la vitesse d'évolution nécessaire pour survivre au changement climatique.

Nos travaux s'insèrent dans le cadre de l'*épidémiologie évolutive*, qui s'intéresse aux dynamiques transitoires dans le cas plus particulier de l'épidémiologie spatialisée, notamment en ce qui concerne [115, 114], où l'on discute de l'influence sur la propagation d'une mutation vers un type virulent. Cette étude est à rapprocher de [201] dans un autre formalisme. Enfin, signalons [147], qui traite plus généralement de l'évolution et de la coévolution entre hôtes et parasites dans le cadre des modèles de lattices.

1.2 Contexte mathématique

Dans cette thèse nous travaillons avec des modèles de réaction-diffusion en espace continu. Nous manipulons soit un nombre fini de densités de population $u_i(t,x)$ associées à différents phénotypes, soit une densité structurée en espace et en trait continu $u(t,x,y)$. Ici, $t \geq 0$ représente le temps, x l'espace "physique", et y l'espace des traits.

1.2.1 Équations de réaction-diffusion scalaires

Environnement homogène

L'étude des équations de réaction-diffusion en biologie remonte aux travaux de Fisher [89] et Kolmogoroff, Petrovsky et Piskunov [141], qui étudièrent presque simultanément l'équation parabolique :

$$\partial_t u - \Delta u = u(1-u) \qquad (t,x) \in \mathbb{R}^+ \times \mathbb{R}^n. \tag{1.5}$$

Ici le terme de gauche $\partial_t u - \Delta u$ représente la diffusion locale des individus (Δ est l'opérateur Laplacien dans $\mathbb{R}^n$; on parle de terme de *diffusion*) et le terme de droite $u(1-u)$ (on parle de terme de *réaction*) représente la dynamique locale de la population. Notons que dans [89, 141], u représente une fraction de la population possédant un allèle bénéfique qui envahit une population supposée à l'équilibre démographique, dans une approche de *génétique des populations* ; du point de vue de la modélisation, il est également possible de

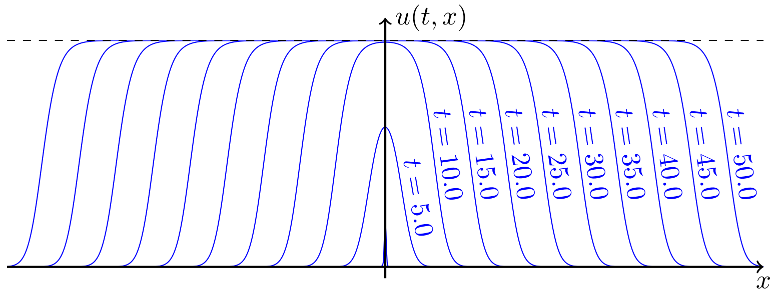


FIGURE 1.2 – Solutions de l'équation de Fisher-KPP partant d'une condition initiale concentrée en $x = 0$

définir u comme une densité de population subissant une dynamique de naissance et mort qui envahit un espace supposé vierge mais avec une capacité d'accueil finie, dans une approche de *dynamique des populations*, analogue à celle proposée dans [190]. Les deux approches sont mathématiquement équivalentes.

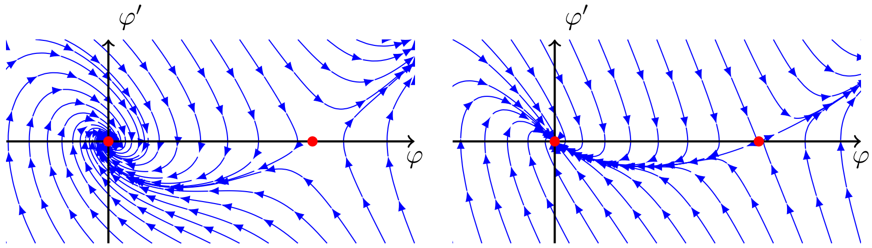
Kolmogoroff, Petrovsky et Piskounov [141] ont montré que le comportement de l'équation (1.5) en temps long peut être caractérisé par l'étude de solutions particulières appelées *fronts progressifs* (en anglais : *traveling waves*). En dimension $n = 1$, et partant d'une condition initiale particulière $u(t = 0, x) = \chi_{(-\infty,0]}$, on peut observer numériquement que la solution $u(t, x)$ de l'équation (1.5) se rapproche d'un profil fixe qui se déplace à vitesse constante le long de l'axe des abscisses (voir aussi Figure 1.2). Mathématiquement, nous traduisons ce phénomène en recherchant des solutions particulières de (1.5) qui sont stationnaires dans un référentiel mobile, dont l'abscisse d'origine est située au point $x - ct$ où c est la *vitesse* du front (c pour *célérité*), *a priori* inconnue. Cela revient à rechercher un profil φ dépendant uniquement de la variable $z = x - ct$ et une vitesse c tels que $u(t, x) := \varphi(x - ct)$ est solution de (1.5) ; autrement dit, (c, φ) est une solution du problème

$$-c\varphi'(z) - \varphi''(z) = \varphi(z)(1 - \varphi(z)), \quad z \in \mathbb{R}. \tag{1.6}$$

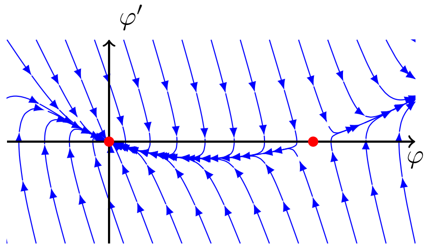
Précisons que le profil recherché φ doit être positif (densité de population) et connecter les états stationnaires 1 en $-\infty$ à 0 en $+\infty$. Un critère pour l'existence de (c, φ) est alors donné par la stabilité asymptotique de ces états dans le plan de phase (φ, φ'). Cette stabilité s'établit en regardant (1.6) dans le *plan de phase* (φ, φ') (cf. Figure 1.3). Le comportement asymptotique au voisinage de $(0, 0)$, en particulier, va nous donner une condition sur c. Celle-ci s'établit en étudiant l'équation linéarisée :

$$-c\psi' - \psi'' = \psi,$$

qui a pour polynôme caractéristique $X^2 + cX + 1 = 0$. Si $c^2 < 4$, les racines



(a) $c = 1$ (b) $c = 2$



(c) $c = 3$

FIGURE 1.3 – Plan de phase de l'EDO des fronts progressifs pour Fisher-KPP. Les points rouges représentent les équilibres.

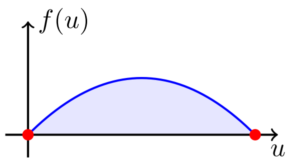
sont complexes et les éventuelles solutions de (1.6) connectant 0 et 1 ne peuvent pas rester positives, et pour $c \leq -2$ l'état 0 est instable au sens des EDO et un couple (c, φ) ne peut donc pas exister. Nous avons donc établi que $c \geq 2$. L'existence d'un front pour tout $c \geq 2$ requiert une analyse plus précise du plan de phase [141]. Les auteurs montrent également que la vitesse atteinte dans le cas d'une condition initiale de type Heaviside est la vitesse minimale $c_* := 2$.

Retenons de l'étude ci-dessus que la vitesse du front critique est complètement déterminée par l'équation linéarisée au voisinage de 0 : dans ce contexte, ce sont les petites populations à l'avant du front qui dirigent la dynamique de propagation. On parle de front *tiré* (*pulled*) pour désigner ce type de dynamique.

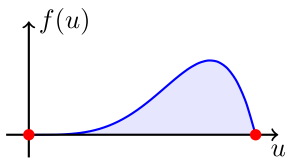
Les résultats de [89, 141] ont été repris et généralisés, notamment dans le cadre des équations de type

$$\partial_t u - Lu = f(u) \tag{1.7}$$

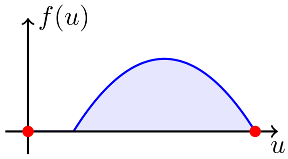
où $x \in \mathbb{R}^n$, L est un opérateur elliptique sur $\mathbb{R}^n$ (modélisant par exemple une diffusion anisotrope), et f est une fonction $\mathbb{R} \to \mathbb{R}$ de type KPP (dont nous détaillerons la définition plus bas). Pour le cas $n = 1$, voir par exemple les travaux de [11, 87, 88] ; en dimension $n > 1$, voir [12, 28, 151], et [202]. Il a été établi, de plus, que toute solution suffisamment localisée converge vers un front progressif de vitesse minimale [48, 123] ($n = 1$).



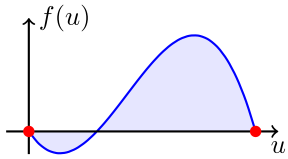
(a) KPP



(b) Monostable dégénéré



(c) Ignition



(d) Bistable

FIGURE 1.4 – Différents types de nonlinéarités

D'autres types de nonlinéarités sont également envisageables dans (1.7). Dans un contexte biologique, on peut distinguer principalement 3 types de nonlinéarités (voir Figure 1.4) pour lesquelles les phénomènes de propagation sont relativement bien compris et ont engendré une vaste littérature :

- les nonlinéarités *monostables* pour lesquelles

$$f(0) = f(1) = 0, f(u) > 0 \text{ pour } u \in (0, 1).$$

  Parmi celles-ci, on distingue les non-dégénérées ($f'(0) > 0$) des dégénérées ($f'(0) = 0$). Les premières incluent les non-linéarités de type KPP satisfaisant

$$u \mapsto \frac{f(u)}{u} \text{ est décroissante}$$

  signifiant que le taux de croissance *per capita* est maximal à petite densité de population (voir Figure 1.4a), que nous considérons dans cette thèse. Les cas dégénérés, par exemple $f(u) \sim_{u\to 0} u^\alpha$ pour $\alpha > 1$, permettent de modéliser un effet Allee [9] (voir Figure 1.4b).

- les nonlinéarités de type *ignition*, pour lesquelles $f(u) = 0$ pour $u \in (0, \theta)$, $f(u) > 0$ pour $u \in (\theta, 1)$ et $f(1) = 0$ (voir Figure 1.4c). Le paramètre θ correspond à une température d'ignition dans des modèles de combustion, mais ce type de nonlinéarités peut également être utilisé pour modéliser un effet Allee plus fort que le précédent, [103, 23, 208].

- enfin, les nonlinéarités de type *bistable* (voir Figure d) pour lesquelles $f(0) = 0$, $f(u) < 0$ pour $u \in (0, \theta)$, $f(u) > 0$ pour $u \in (\theta, 1)$, et $f(1) = 0$, dont le prototype est la nonlinéarité cubique

$$f(u) = u(u - \theta)(1 - u).$$

Typiquement, les cas monostables conduisent à une demi-droite de vitesses admissibles pour les fronts, alors que la vitesse des fronts est unique pour les cas ignition et bistable [11, 88, 100]. Notons que, alors que le front critique KPP est tiré, les fronts ignition ou bistable sont *poussés* : la vitesse n'est pas donnée par le linéarisé en 0 [102, 179].

Jusqu'à présent nous avons discuté de la vitesse des fronts associés à (1.7). Il existe une autre notion utile pour étudier la propagation des solutions des équations de type (1.7), qui est la *vitesse de propagation* (en anglais : *spreading speed*). Plaçons-nous pour simplifier en dimension $n = 1$; si elle existe, la vitesse de propagation est l'unique $c_{prop} > 0$ telle que pour toute condition initiale u_0 à support compact, vérifiant $0 \leq u_0 \leq 1$ et $u_0 \not\equiv 0$, la solution $u(t,x)$ du problème de Cauchy vérifie

$$\limsup_{t\to\infty} \sup_{|x|<ct} |u(t,x) - 1| = 0 \quad \text{pour tout } c < c_{prop}$$

et

$$\limsup_{t\to\infty} \sup_{|x|>ct} u(t,x) = 0 \quad \text{pour tout } c > c_{prop}.$$

Cette notion a été introduite par Aronson et Weinberger [12] et développée par Weinberger [202] dans un cadre très général. Si c_* désigne la vitesse minimale des fronts pour la même équation, nous avons en général

$$c_{prop} \leq c_*.$$

Dans [202], l'auteur détaille des conditions sous lesquelles les deux vitesses sont égales, notamment des conditions de *déterminisme linéaire* de la vitesse, englobant le cas KPP.

Notons qu'une éventuelle queue de distribution de la condition initiale peut fortement changer la dynamique d'invasion, soit $c_{prop} = c_{prop}(u_0)$, possiblement non définie ou infinie. Ainsi, certaines queues exponentielles conduisent à $c_{prop}(u_0) > c_*$ dans des modèles KPP. D'autre part, des travaux plus récents s'intéressent à une invasion à "spreading oscillant" [122], une accélération induite par des queues lourdes [124], ou une compétition "queues lourdes vs. effet Allee" [1].

Environnement hétérogène, fronts pulsatoires

Les hétérogénéités spatiales jouent un rôle important lors d'invasions biologiques, ou dans les systèmes hôtes-parasites. Afin de comprendre l'influence de cette structure, on introduit dans (1.7) une dépendance spatiale dans la nonlinéarité. On s'intéresse ainsi à

$$\partial_t u - Lu = f(x,u), \tag{1.8}$$

où la fonction $f(x,u)$ prend en compte à la fois l'hétérogénéité de l'environ-

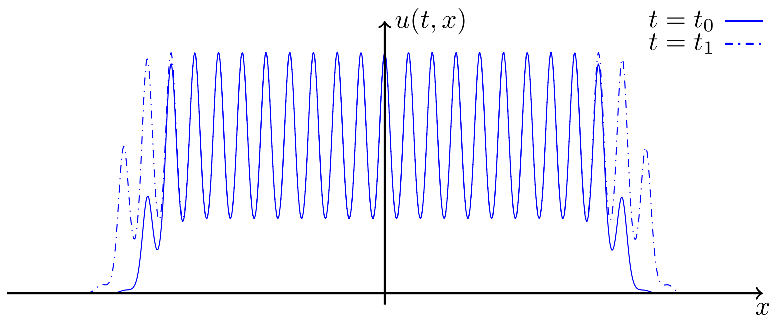


FIGURE 1.5 – Exemple de solution du problème de Cauchy (1.8) à deux temps proches $t_0 < t_1$, pour la nonlinéarité $f(x,u) = \left(\frac{1}{2} + \cos(x)\right) u - u^2$ et $L = \partial_{xx}$.

nement (par la dépendance en la variable d'espace x) et la dynamique de la population (par la dépendance dans la densité de population u). Notons qu'il est également possible d'autoriser l'opérateur elliptique L à dépendre de la variable d'espace, pour prendre en compte par exemple des différences dans la mobilité des individus selon leur position. Cette équation a été étudiée dans les travaux de Freidlin et Gertner [107], dans le cas d'une nonlinéarité de type KPP en environnement aléatoire ou périodique, par des techniques probabilistes. Les techniques EDP pour de tels problèmes sont plus récentes. Ainsi, Xin [208, 206, 207, 205] considère des nonlinéarités de type ignition et bistable en environnement périodique. Pour des modèles périodiques KPP, on renvoie aux travaux pionniers de Weinberger [203], Berestycki et Hamel [18], et également [20], ainsi que Liang, Lin et Matano pour des coefficients potentiellement singuliers [146].

Le cas particulier de l'environnement périodique est particulièrement intéressant car on peut y définir un analogue des fronts progressifs. Il est bien entendu que les variations du terme de réaction interdisent de calquer la notion de fronts sur celle des fronts progressifs (voir Figure 1.5), mais des simulations numériques montrent une certaine régularité dans le comportement en temps long des solutions. Si pour tout u, $x \mapsto f(x,u)$ est de période L, nous appellerons *front pulsatoire* voyageant à la vitesse $c \in \mathbb{R}$ une solution particulière de (1.8) définie pour $(t,x) \in \mathbb{R} \times \mathbb{R}$ (par simplicité nous nous plaçons en dimension 1) et vérifiant la propriété suivante :

$$\forall (t,x) \in \mathbb{R}^2, \qquad u\left(t + \frac{L}{c}, x\right) = u(t, x - L)$$

et vérifiant les conditions aux limites appropriées (disons, sans rentrer dans plus de détails, $u \to 0$ quand $t \to -\infty$, $u \to p(x)$ quand $t \to +\infty$ où p est une solution stationnaire non triviale). Une définition plus précise dans le cas KPP est présentée par exemple dans [20]. Cela revient à postuler l'existence d'un profil $\varphi(s,x)$ L-périodique en x et tel que

$$u(t,x) := \varphi(x-ct,x)$$

soit solution de (1.8). Plongeant cet ansatz dans l'équation, on obtient non pas une EDO (cf les fronts progressifs), mais une EDP elliptique qui, de plus, est dégénérée.

De ce fait, même dans le cas scalaire, l'analyse des fronts pulsatoires est nettement plus ardue que celle des fronts progressifs. Néanmoins, des similarités existent. En particulier, dans le cas d'une nonlinéarité de type KPP, on sait en général déterminer si les fronts existent et, dans ce cas, construire des fronts monotones dans le référentiel mobile, pour une demi-droite de vitesses admissibles $[c_*, +\infty)$. De plus, la vitesse du front critique est déterminée par un critère de stabilité de l'état stationnaire 0, cette fois-ci dans un espace plus complexe que le plan de phase.

Weinberger [203] a également formalisé dans ce contexte la notion de vitesse de propagation, et on retrouve des conditions sous lesquelles la vitesse de propagation est égale à la vitesse minimale des fronts.

L'un des outils mathématiques à la source d'une grande partie des résultats pour les équations scalaires est le *principe de comparaison*, qui stipule que l'ordre des solutions de (1.8) se conserve au cours du temps. Autrement dit, prenons deux populations initiales $u_0(x) \leq u_1(x)$, et intéressons nous aux population respectives $u_0(t,x)$ et $u_1(t,x)$ obtenue après un temps t, chacune des deux populations subissant la même dynamique (par exemple (1.8), ou plus simplement (1.5)). Alors, d'après le principe de comparaison, $u_0(t,x) \leq u_1(t,x)$. Lorsque ce principe tombe en défaut, des dynamiques plus complexes peuvent intervenir et de nouvelles techniques sont souvent nécéssaires pour étudier le comportement des solutions.

1.2.2 Équations de réaction-diffusion non-locales

Dans cette section nous rappelons des généralités sur les équations *non-locales*. Typiquement, on introduit des effets non-locaux dans la diffusion (conservant habituellement la comparaison), ou dans la réaction, annihilant (souvent) le principe de comparaison. Nous incluons les systèmes d'équations de réaction-diffusion dans cette catégorie car ils possèdent de nombreuses similarités avec ce type d'équations ; par ailleurs, un système peut souvent être considéré comme une équation scalaire dépendant d'une variable discrète supplémentaire, justifiant *de facto* le caractère non-local des systèmes ne se réduisant pas à une collection d'équations découplées.

Le cas des systèmes

Pour étudier des phénomènes de propagation dans lesquels plusieurs espèces interagissent entre elles, nous pouvons utiliser le formalisme introduit par

Fisher et Kolmogoroff et al (1.5) dans le cadre des systèmes de réaction-diffusion. Des travaux pionniers ont été réalisés à ce sujet par Tang et Fife [193] et Gardner [99], qui envisagent des systèmes *compétitifs* de la forme

$$\begin{cases} \partial_t u = d_1 u_{xx} + u f(u,v) \\ \partial_t v = d_2 v_{xx} + v g(u,v) \end{cases} \tag{1.9}$$

où $f_v \leq 0$ et $g_u \leq 0$. Ils prévoient l'existence de fronts de propagation dans deux cas différents : Tang et Fife s'intéresse à l'invasion d'un espace vierge, et Gardner envisage le remplacement d'une espèce par l'autre. Ils utilisent tous deux une méthode de plan de phase.

Pourtant, l'analyse de la propagation pour des systèmes comme (1.9) est bien plus difficile que celle de (1.5). L'une des raisons est que l'analyse de la propagation pour les équations de type (1.7) s'appuie en grande partie sur la richesse des outils mathématiques des théories elliptique et parabolique, comme le principe de comparaison, l'inégalité de Harnack, etc... qui n'ont habituellement pas d'équivalent pour les systèmes [55].

Dans le cas favorable des systèmes *coopératifs* (définis plus bas), on retrouve des résultats analogues à ceux du cas scalaire, tout particulièrement dans le sous-cas des systèmes *fortement couplés*. En général, un système (linéaire ici, pour simplifier) d'équations de réaction-diffusion s'écrit :

$$\partial_t \mathbf{u} - \mathbf{L}\mathbf{u} = A(x)\mathbf{u} \tag{1.10}$$

où $\mathbf{u} := \begin{pmatrix} u_1 \\ \vdots \\ u_d \end{pmatrix} \in C^2(\mathbb{R}^+ \times \mathbb{R}^n, \mathbb{R}^d)$, $\mathbf{L}$ est une matrice diagonale d'opérateurs elliptiques, et $A(x)$ est un champ de matrices de dimension d. Celui-ci est dit *coopératif* (et avec lui le système (1.10)), si tous ses coefficients extra-diagonaux sont positifs au sens large ; il est de plus *fortement couplé* si ces coefficients sont de plus strictement positifs (pour une définition plus précise, voir par exemple [55]). Pour ces systèmes, il existe des résultats qui sont l'analogue de ceux de Weinberger : Lui [149] donne une première généralisation et des propriétés des vitesses de propagation, étendues par Weinberger, Lewis et Li [204]. Ces résultats sont fortement liés à la présence de théorèmes de comparaison et d'une boîte à outils mathématiques similaire à ceux existant dans le cas scalaire.

Nos travaux [114, 7] s'insèrent dans le cadre plus général des systèmes coopératifs au voisinage de l'état stationnaire trivial, mais non coopératifs en général. Le système considéré dans [114], par exemple,

$$\begin{cases} u_t - u_{xx} = u(1-(u+v)) + \mu(v-u) =: F(u,v) \\ v_t - v_{xx} = rv\left(1 - \frac{u+v}{K}\right) + \mu(u-v) =: G(u,v) \end{cases} \tag{1.11}$$

où $r > 1$, $0 < K < 1$ et $0 < \mu < K$, est bien coopératif lorsque $(u, v) \approx (0, 0)$, grâce aux termes de mutations $\pm\mu(u - v)$; en revanche, il n'est pas *globalement* coopératif car :

$$\partial_v F(u, v) = \mu - u, \quad \partial_u G(u, v) = \mu - \frac{r}{K} v,$$

et $\partial_v F(u, v)$, $\partial_u G(u, v)$, deviennent négatifs dès que $u > \mu$, $v > \frac{K}{r}\mu$, respectivement ; le système devient compétitif lorsque ces deux conditions sont satisfaites. Néanmoins, malgré l'absence de comparaison, nous avons pu, entre autres, construire des fronts progressifs grâce à des méthodes topologiques, et donner la vitesse minimale de ces fronts.

L'étude des systèmes localement coopératifs est un domaine actif de la recherche actuelle. Wang [200] donne des conditions sous lesquelles il existe une vitesse de propagation pour une certaine classe de systèmes non-coopératifs, mais encadrés par deux systèmes coopératifs. Ces conditions ont récemment été utilisées par Morris, Börger et Crooks [156] pour étudier un système de compétition-mutations. Mentionnons également le travail de Girardin [109], qui donne le comportement en temps long de systèmes localement coopératifs dans le cadre des nonlinéarités de type KPP.

Dans un cadre périodique, l'étude des fronts pour les systèmes de type KPP est un défi majeur car, à l'absence de comparaison, s'ajoute la difficulté "opérateur elliptique dégénéré" inhérente aux fronts pulsatoires. Dans cette optique, nous étudions dans [7] une version hétérogène de (1.11) :

$$\begin{cases} u_t - u_{xx} = u(r_u(x) - \gamma_u(x)(u + v)) + \mu(x)(v - u) \\ v_t - v_{xx} = v(r_v(x) - \gamma_v(x)(u + v)) + \mu(x)(u - v), \end{cases}$$

où les coefficients $r_u, r_v, \gamma_u, \gamma_v, \mu$ sont des fonctions L-périodiques de l'espace. A notre connaissance, les travaux s'en rapprochant sont les articles de Yu et Zhao [211] dans un cadre purement compétitif, et ceux de Fang, Yu et Zhao [83], dans un cadre monotone. En particulier, notre travail [7] semble être la première construction de fronts pulsatoires avec une nonlinéarité de type KPP dans un cadre dépourvu de théorème de comparaison (voir [59, 130] pour une construction avec une nonlinéarité de type ignition). Signalons enfin que, à notre connaissance, il n'y a pas d'équivalent hétérogène des résultats de [204], même dans un cadre coopératif, ce qui indique que les questions ouvertes sur ce sujet restent nombreuses.

Équations intégro-différentielles

Comme indiqué ci-dessus, les effets non-locaux peuvent d'abord être introduits dans la dispersion. Si le déplacement des individus peut les envoyer à "grande distance", la probabilité de passer de la position x à la position

y peut être modélisée par un noyau de convolution $J(x-y)$, où J est une densité de probabilité. L'équation modèle s'écrit alors

$$u_t = (J * u - u) + f(x,u).$$

L'étude des fronts progressifs et/ou pulsatoires est due à Coville et Dupaigne [63, 64], Coville [60] et Coville, Dávila et Martínez [62]. D'autre part, si J est à queues lourdes, les invasions se font à vitesse sur-linéaire [101] ([57] pour une diffusion fractionnaire) dans le cas KPP, mais cette accélération peut être annihilée par un effet Allee faible [4] ([116] pour une diffusion fractionnaire). Notons que, contrairement à nos problèmes ci-dessous, le principe de comparaison s'applique à de tels modèles.

Considérons maintenant l'équation de Fisher-KPP non-locale [49, 111]

$$u_t = u_{xx} + u\left(1 - \phi * u\right), \tag{1.12}$$

où ϕ est un noyau positif de masse 1. Cette équation intervient quand on considère que deux individus distants peuvent être en compétition, contrairement à (1.5) où la compétition est uniquement locale. Si ϕ est la masse de Dirac, on retrouve formellement (1.5). Cependant, moins le noyau ϕ est "concentré", plus les chances de déstabiliser l'état stationnaire 1 existent. Pour cette raison, l'identification du comportement d'un front en $-\infty$ est un réel défi. Malgré cela, les auteurs de [25] réalisent la première construction non perturbative de fronts pour l'équation (1.12), ouvrant ainsi une voie pour ces modèles. L'idée consiste à se ramener en domaine borné où un argument de degré est utilisé, ce qui requiert de fines estimations *a priori*. Du fait de la difficulté évoquée ci-dessus, la condition de bord en $-\infty$ pour la définition d'un front est affaiblie : typiquement, on demande $\liminf_{z\to-\infty} u(z = x - ct) > 0$ et pas $u(-\infty) = 1$.

D'autre part, les modèles intégro-différentiels sont particulièrement adaptés pour traiter des populations *structurées en trait*, dans lesquelles les individus peuvent présenter un comportement différent suivant la valeur d'un trait phénotypique héritable, comme la taille des pattes des crapauds-buffles d'Australie, dont l'évolution peut être modélisée par :

$$u_t = \theta u_{xx} + u_{\theta\theta} + ru\left(1 - \int_{\underline{\theta}}^{\overline{\theta}} u(t,x,\theta')d\theta'\right).$$

Ici, $x \in \mathbb{R}$ représente l'espace physique, $\theta \in [\underline{\theta}, \overline{\theta}] \subset (0, +\infty)$ représente l'espace des traits. Le terme $u_{\theta\theta}$ modélise les mutations et le trait θ rétroagit sur le coefficient de diffusion spatiale, qui modélise la mobilité des individus. Enfin, le terme de compétition est non-local en le trait. Pour l'étude de ce modèle et des variantes, on renvoie à [43, 42, 194, 46, 45].

Un autre exemple est l'étude de Alfaro, Coville et Raoul [5], qui propose l'équation

$$n_t = n_{xx} + n_{yy} + n\left(r(y - Bx) - \int_{\mathbb{R}} n(t,x,y')dy'\right)$$

pour étudier l'évolution de l'aire de répartition d'espèces affrontant un gradient environnemental. Ici le trait y est non borné, et le taux de croissance est maximal le long de $y = Bx$, signifiant qu'il faut adapter son trait à sa position spatiale. Signalons les travaux [2, 17] sur des problèmes reliés.

Dans un travail en cours de rédaction, nous étudions les phénomènes de propagation de l'équation non-locale :

$$u_t = u_{xx} + \mu(M \star u - u) + u(a(y) - K \star u), \tag{1.13}$$

où $x \in \mathbb{R}$ représente un espace linéaire, $y \in \overline{\Omega}$ est un trait évoluant dans un domaine borné régulier $\Omega \subset \mathbb{R}^d$, $a(y)$ est une fonction $\overline{\Omega} \to \mathbb{R}$, M et K sont des noyaux de mutation et compétition, positifs et bornés sur $\overline{\Omega} \times \overline{\Omega}$, et l'opération $\star$ est définie par

$$(M \star u)(t, x, y) := \int_{\Omega} M(y, z)u(t, x, z)dz.$$

Sous certaines conditions sur a, la valeur propre principale n'est pas associée à une fonction propre mais à une famille de mesures [61]. Dans ce cas, nous nous attendons à ce que les fronts progressifs associés à l'équation (1.13) possèdent une partie singulière. De tels fronts sont construits dans le cas où le noyau de compétition K ne dépend pas de y ; dans le cas général, nous construisons des fronts progressifs u tels que pour presque tout $z = x - ct$, $u(z, \cdot)$ est une mesure positive sur $\overline{\Omega}$. Il s'agit, à notre connaissance, de la première construction de fronts au sens des mesures.

1.3 Travaux effectués dans cette thèse

1.3.1 Résumé du chapitre 2 : Construction et propriétés qualitatives des fronts progressifs pour un modèle en épidémiologie évolutive

Ce chapitre a fait l'objet d'une publication en collaboration avec Gaël Raoul dans *Journal of Differential Equations* [114]. Nous présentons ici une analyse mathématique, dont une analyse plus poussée sur le plan biologique sera présentée au chapitre 3.

Dans ce travail nous étudions l'existence de fronts progressifs pour l'équation (1.11). Plus précisément, nous étudions la solvabilité du problème :

$$\begin{cases} -cw' - w'' = w(1 - (w + m)) + \mu(m - w) \\ -cm' - m'' = rm\left(1 - \frac{w+m}{K}\right) + \mu(w - m) \end{cases} \tag{1.14}$$

avec les conditions aux limites :

$$\liminf_{x \to -\infty} w(x) + m(x) > 0, \qquad \lim_{x \to +\infty} w(x) + m(x) = 0. \tag{1.15}$$

Cette équation intervient dans la modélisation de la propagation d'un pathogène pouvant muter avec taux μ entre deux phénotypes : un type *résident* (en anglais : *wild type*), peu virulent, et un type *mutant* très virulent. Les hypothèses sur r et K correspondent à une hypothèse classique de compromis (*trade-off*) entre la virulence et la capacité d'accueil : un accroissement dans la virulence $r > 1$ est "compensé" par une capacité d'accueil affaiblie $K < 1$ (voir, par exemple, Alizon *et al* [8]).

Existence de fronts progressifs

Notre premier résultat est le suivant :

Théorème 1.3.1 (Fronts de compétition-mutations)**.** *Sous certaines hypothèses sur les coefficients r K et μ, il existe un triplet $(c, w, m) \in \mathbb{R} \times C^\infty(\mathbb{R}) \times C^\infty(\mathbb{R})$ vérifiant l'équation* (1.14)*, les conditions aux limites* (1.15) *et*

$$\forall x \in \mathbb{R}, m(x) \in (0, K), w(x) \in (0, 1)$$

$$c = c_* := \sqrt{2\left(1 + r - 2\mu + \sqrt{(r-1)^2 + 4\mu^2}\right)}. \tag{1.16}$$

De plus, c_* est la vitesse minimale des fronts : pour $0 \le c < c_*$, il n'existe pas de couple (w, m) de fonctions positives satisfaisant (1.14) *et* (1.15)*.*

Ce résultat assure l'existence de fronts progressifs pour l'équation (1.11) et donne une formule pour la vitesse minimale des fronts (1.16). La preuve repose principalement sur un argument de degré topologique. La difficulté principale est ici l'absence de théorème de comparaison, qui rend inadaptée la méthode des itérations monotones et complique l'obtention d'estimations *a priori.*

Le schéma de la preuve est inspiré de [25]. Nous en rappelons ici les axes principaux. Tout d'abord, nous étudions le problème localisé sur $(-a, a)$:

$$\begin{cases} -cw' - w'' = w(1 - (w + m)) + \mu(m - w) \\ -cm' - m'' = rm\left(1 - \frac{w+m}{K}\right) + \mu(w - m) \\ (w(-a), m(-a)) = (w^*, m^*) \\ (w(a), m(a)) = 0 \end{cases} \tag{1.17}$$

où (w^*, m^*) est l'unique état stationnaire associé à (1.14). Nous étudions la solvabilité de (1.17) pour a assez grand conjointement à la condition de normalisation :

$$\sup_{x \in (-a_0, a_0)} w(x) + m(x) = \nu \tag{1.18}$$

pour un ν assez petit et un a_0 assez grand fixés. Le rôle de (1.18) est de contrôler les vitesses admissibles. Plus précisément, pour $a \gg a_0$ nous avons les estimations a priori suivantes :

- si $c = 0$ alors toute solution positive de (1.17) vérifie

$$\sup_{x\in(-a_0,a_0)} w(x) + m(x) > \nu \ ;$$

- si $c \geq c_*$ alors toute solution positive de (1.17) vérifie

$$\sup_{x\in(-a_0,a_0)} w(x) + m(x) < \nu.$$

Le reste de la preuve consiste à calculer le degré topologique de Leray-Schauder associé à l'équation (1.17) pour montrer l'existence d'une solution satisfaisant de plus (1.18). Plus précisément, nous écrivons une solution de (1.17) - (1.18) comme un point fixe de l'opérateur :

$$F(c,w,m) := \left(c + \nu - \sup_{x\in(-a_0,a_0)} (\tilde{w}(x) + \tilde{m}(x)), \tilde{w}, \tilde{m} \right)$$

où $(\tilde{w}, \tilde{m})$ sont définis par le système :

$$\begin{cases} -c\tilde{w}' - \tilde{w}'' = w(1-(w+m)) + \mu(m-w) \\ -c\tilde{m}' - \tilde{m}'' = rm\left(1 - \frac{w+m}{K}\right) + \mu(w-m) \\ (\tilde{w}(-a), \tilde{m}(-a)) = (w^*, m^*) \\ (\tilde{w}(a), \tilde{m}(a)) = 0. \end{cases}$$

Dans un ouvert adapté de $\mathbb{R}\times C^0(-a,a)\times C^0(-a,a)$, nous nous ramenons par homotopies successives (en "déformant" le terme de réaction) à un problème découplé en (c,w,m) pour lequel le degré est calculable explicitement et non nul. Cela montre l'existence d'une solution (c,w,m) au problème (1.17) satisfaisant (1.18). Nous pouvons alors passer à la limite $a \to \infty$ et récupérer une solution de (1.14) sur $\mathbb{R}$ qui satisfait toujours (1.18), et qui est donc non triviale. Nous utilisons alors (1.18) pour montrer que la solution construite satisfait les conditions aux limites (1.15). Cela montre l'existence d'un front progressif associé à (1.14). De plus, la condition de normalisation montre que le front (c,w,m) construit satisfait $c > 0$, et par construction $c \leq c_*$. Enfin, en utilisant une sous-solution adaptée, nous montrons que c_* est la vitesse minimale des fronts et nous avons donc $c = c_*$ pour le front construit.

Propriétés qualitatives du front progressif construit

Notre deuxième résultat concerne le comportement qualitatif des fronts construits dans le Théorème 1.3.1.

Théorème 1.3.2 (Comportement en $-\infty$ et forme des fronts)**.** *Sous certaines hypothèses sur r, K et μ, le front (c_*, w, m) construit au théorème 1.3.1 satisfait*

$$\lim_{x\to-\infty} w(x) = w^*, \qquad \lim_{x\to-\infty} m(x) = m^*$$

où (w^*, m^*) est l'unique zéro du terme de réaction de (1.14) *dans le domaine* $(0,1] \times (0,K]$.

De plus, cette solution (w,m) vérifie l'une des propriétés suivantes :

1. *w est décroissante sur $\mathbb{R}$, et il existe $\bar{x} \in (-\infty, 0)$ tel que m est croissante sur $(-\infty, \bar{x})$ et décroissante sur $(\bar{x}, +\infty)$.*
2. *m est décroissante sur $\mathbb{R}$, et il existe $\bar{x} \in (-\infty, 0)$ tel que w est croissante sur $(-\infty, \bar{x})$ et décroissante sur $(\bar{x}, +\infty)$.*
3. *w et m sont décroissantes sur $(-\infty, +\infty)$.*

Enfin, il existe $\mu_0 = \mu_0(r,K) > 0$ tel que pour $\mu < \mu_0$, il existe une solution satisfaisant 1.

Nous prouvons ce théorème par un argument de plan de phase sur le problème localisé (1.17), en examinant les trajectoires possibles reliant l'état stationnaires (w^*, m^*) à $(0,0)$. Ces propriétés passent ensuite naturellement à la limite $a \to \infty$.

Convergence du profil w vers un front sur-critique de l'équation de Fisher-KPP

Notre troisième résultat concerne le comportement du profil w quand la capacité d'accueil du mutant est petite : $K \to 0$. Nous montrons que le profil w tend vers un front de l'équation classique de Fisher-KPP qui voyage à une vitesse plus grande que la vitesse minimale.

Théorème 1.3.3 (Convergence vers KPP sur-critique)**.** *Soit $r \in (1, +\infty)$, $K \in (0,1)$, $\mu \in (0,K)$ et (c_*, w, m) une solution positive de* (1.14) *satisfaisant* (1.15). *Il existe des constantes $C = C(r)$, $\beta = \beta(r) \in \left(0, \frac{1}{2}\right)$ et $\varepsilon > 0$, et un front de l'équation de Fisher-KPP voyageant à vitesse $c_0 := 2\sqrt{r}$, c'est à dire un profil u satisfaisant*

$$\begin{cases} -c_0 u' - u'' = u(1-u) \\ \lim_{x\to-\infty} u(x) = 1, \quad \lim_{x\to+\infty} u(x) = 0, \end{cases}$$

tels que si $0 < \mu < K < \varepsilon$, alors

$$\|w - u\|_{L^\infty} \leq CK^\beta.$$

Nous prouvons ce théorème en construisant des sur- et sous-solutions de l'équation satisfaite par le résident w, et qui convergent uniformément vers un front de Fisher-KPP sur-critique.

1.3.2 Résumé du chapitre 3 : Évolution de la virulence au front de propagation d'une épidémie

Ce chapitre a fait l'objet d'une publication en collaboration avec Gaël Raoul et Sylvain Gandon dans *Evolution* [115].

Dans ce travail nous discutons de la propagation d'un pathogène possédant un fort taux de mutation pouvant faire varier son phénotype entre un type *résident* et un type *mutant*. Cette étude s'insère dans le cadre de l'épidémiologie évolutive spatialisée, puisque nous supposons une structure spatiale de la population et un couplage entre la dynamique épidémiologique et la dynamique évolutive du pathogène.

La prévision de la vitesse de propagation dans l'espace est centrale en biologie de l'invasion [89, 141, 190]. Sous l'hypothèse simplificatrice d'un environnement homogène, les modèles de diffusion permettent d'obtenir des prédictions sur la vitesse asymptotique de propagation [188]. Dans le cas de modèles logistiques homogènes en espace, la population ressemble asymptotiquement à un front progressif voyageant à une vitesse $c = 2\sqrt{\sigma r}$, où σ est la constante de diffusion et r le taux d'accroissement de l'espèce. Perturber les hypothèses sous-jacentes conduit à une modification quantitative de cette vitesse. Par exemple, supposer une hétérogénéité spatiale peut accélérer ou freiner l'invasion [188, 187, 80] ; modifier la forme du noyau de dispersion peut avoir des conséquences encore plus importantes sur la propagation. Des noyaux de dispersion à queues lourdes peuvent en effet conduire à une propagation dont la vitesse croît avec le temps [143].

Dans de nombreuses études, nous retrouvons l'hypothèse que la dynamique évolutive peut être négligée, car elle intervient à une échelle de temps plus lente [164]. Il existe toutefois des exemples d'invasions durant lesquelles l'évolution agit très rapidement [164, 165, 54]. En particulier, les populations virales, qui sont souvent caractérisées par un grand nombre d'individus et de très forts taux de mutation, sont susceptibles de présenter une évolution suffisamment rapide pour affecter la propagation de l'épidémie [132].

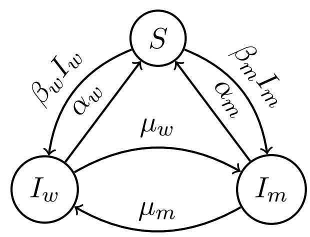
D'autres études se focalisent sur les interactions entre structure spatiale et évolution [40, 41, 148, 147]. Nombre d'entre elles considèrent l'évolution à long terme de la population, après que cette dernière a atteint son équilibre endémique. La théorie de l'épidémiologie évolutive, quant à elle, cherche à suivre les dynamiques transitoires des pathogènes dans des milieux bien mélangés [72, 70, 30].

Ici nous étendons les résultats des études précédentes en suivant l'épidémiologie et l'évolution pendant la propagation spatiale d'une épidémie. Nous développons un modèle de réaction-diffusion pour appréhender l'évolution de la virulence et son impact sur la vitesse de propagation d'une épidémie dans une population d'hôtes homogène en espace. Nous explorons la robustesse de nos conclusions dans d'autres scénarios épidémiologiques et pour d'autres cycles de vie du parasite. Enfin, nous comparons nos prévisions théoriques à des mesures obtenues par simulation, et nous explorons l'impact de la démographie et de la stochasticité sur la dynamique d'invasion.

Modèle

Notre point de départ est un modèle épidémiologique classique dans lequel chaque hôte peut être dans un état susceptible ou infecté. Nous supposons qu'il y a exactement deux types de pathogènes : un type *résident* w (en anglais : *wild type*) et un type *mutant* m. Chacune des souches w et m est caractérisée par des traits spécifiques : son taux de transmission β_i ($i \in \{w, m\}$) et son taux de mortalité α_i ($i \in \{w, m\}$). Nous introduisons également pour chaque souche un taux de mutation μ_w et μ_m, respectivement, qui correspond au taux (supposé constant) auquel une infection par le type w se transforme en une infection de type m et réciproquement. Nous supposons que, chaque fois qu'un hôte est infecté par les deux souches, l'une d'entre elles élimine l'autre par exclusion compétitive (en particulier, nous écartons le cas des surinfections).

Le cycle de vie des pathogènes peut être schématisé de la manière suivante :



où S représente la quantité d'hôtes sains, I_w représente la quantité d'hôtes infectés par le pathogène résident et I_m représente la quantité d'hôtes infectés par le pathogène mutant.

Précisons maintenant la structure spatiale de la population d'hôtes. Ici, les hôtes sont répartis de manière homogène sur une droite, et diffusent avec une constante de diffusion σ. Pour simplifier, nous travaillons sour l'hypothèse que chaque mort est immédiatement remplacé par un individu sain S. Dans notre modèle, la quantité totale d'hôtes $S + I_w + I_m = N$ est donc constante. Enfin, nous supposons que l'impact de l'infection sur le taux de diffusion σ est négligeable. Notre modèle peut donc s'écrire comme un système d'équations de réaction-diffusion :

$$\begin{cases} \frac{\partial I_w}{\partial t} = \sigma \frac{\partial^2 I_w}{\partial x^2} + r_w I_w \left(1 - \frac{I_w + I_m}{K_w}\right) + \mu_m I_m - \mu_w I_w \\ \frac{\partial I_m}{\partial t} = \sigma \frac{\partial^2 I_m}{\partial x^2} + r_m I_m \left(1 - \frac{I_m + I_m}{K_m}\right) + \mu_w I_w - \mu_m I_m \end{cases} \tag{1.19}$$

où $r_i := \beta_i - \alpha_i$ et $K_i := N\left(1 - \frac{\alpha_i}{\beta_i}\right)$. Remarquons que le taux de reproduction de base de chaque souche prise isolément est $R_{0,i} = \frac{\beta_i}{\alpha_i}$, et nous avons

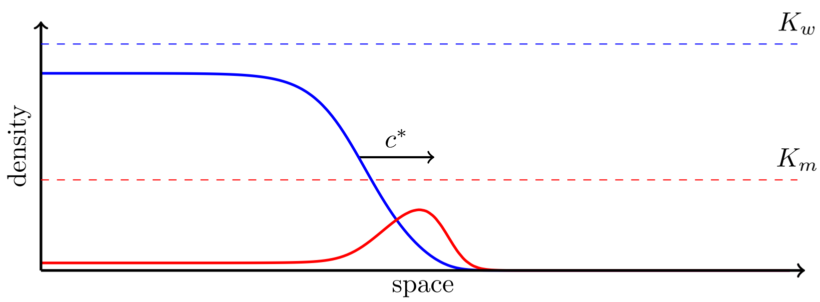


FIGURE 1.6 – Forme typique des fronts du système (1.19) (en bleu : I_w ; en rouge : I_m).

donc un lien entre $R_{0,i}$ et K_i :

$$K_i = N\left(1 - \frac{1}{R_{0,i}}\right).$$

Enfin, nous supposons que la souche m est plus virulente que la souche w,et que le taux d'accroissement de la population mutante est plus grand que celui de la population résidente, ce qui se traduit par $r_w < r_m$, $R_{0,w} > R_{0,m}$ et $K_w > K_m$; par ailleurs, le taux d'accroissement de la population mutante est plus grand que celui de la population résidente : $r_w < r_m$.

Ce scénario est classique pour étudier l'évolution de la virulence [93, 8]. L'originalité du présent modèle est d'étudier conjointement la dynamique épidémiologique et évolutive dans un contexte spatialisé.

Résultats

Vitesse de propagation de l'épidémie. Les solutions numériques de (1.19) ont une forme caractéristique, et qui reste stable pour de nombreuses valeurs de paramètres (voir Figure 1.6). La souche mutante est prévalente à l'avant du front grâce à son plus fort taux d'accroissement r_m. À l'arrière du front, en revanche, on retrouve l'équilibre endémique classique où w est prévalent grâce à son plus fort taux de reproduction de base $R_{0,w}$.

En utilisant une approximation linéaire à l'avant du front, nous obtenons une formule explicite pour la vitesse de propagation :

$$c_* = \Bigg(2\sigma\Big(r_w + r_m - (\mu_w + \mu_m) + \sqrt{(r_w - r_m)^2 + 2(r_w - r_m)(\mu_m - \mu_w) + (\mu_w + \mu_m)^2}\Big)\Bigg)^{\frac{1}{2}}.$$

Lorsque μ_m et μ_w sont petits, nous trouvons l'approximation suivante :

$$c_* = c_m - \kappa(\mu_w, \mu_m) + o(\mu_w, \mu_m)$$

où $c_m = 2\sqrt{\sigma r_m}$ est la vitesse de la souche mutante isolée, et κ est le coût de la mutation en vitesse :

$$\kappa(\mu_w, \mu_m) = \mu_m \sqrt{\frac{\sigma}{r_m}}.$$

Par cette formule, nous voyons que la vitesse de propagation de l'épidémie générée par les deux pathogènes est proche de celle que l'on observerait en considérant le mutant seul ; la dynamique de l'épidémie au voisinage du front de propagation est donc dirigée par le trait mutant.

Aire de répartition du mutant. Pour mieux comprendre l'épidémie, nous avons établi une approximation de l'aire de répartition du mutant. Celle-ci est définie comme la distance a_m entre la position du premier individu infecté et le dernier point d'espace où le mutant est plus abondant que le résident.

Nous avons établi :

$$a_m \approx 2\sqrt{\frac{\sigma}{r_m}} \log(K_m) - \frac{2\sqrt{\sigma r_m}}{\left(1 - \frac{K_m}{K_w}\right) r_w} \log \mu_m.$$

Cette approximation correspond qualitativement aux mesures effectuées sur les solutions numériques de (1.19).

Équilibre de mutation-sélection à l'arrière du front. Sous l'hypothèse que les taux de mutation restent petits par rapport aux taux d'accroissement respectifs des populations, nous retrouvons à l'arrière du front un résultat classique en génétique des populations [66] :

$$p_{eq} \approx \frac{\mu_w}{s},$$

où p_{eq} désigne la fraction de mutants dans la population infectée totale et $s = \left(\frac{K_w}{K_m} - 1\right) r_m$ mesure la force de la sélection.

Simulations d'un modèle stochastique similaire. Nous avons également testé la cohérence du modèle déterministe (1.19) dans une version stochastique. Nous considérons ici un nombre fini d'hôtes répartis sur des sites distants de h. Nous supposons que chaque site accueille exactement N hôtes. Enfin, nous modélisons les différents événements impactant la population (infection, mort, diffusion, mutation) par des horloges exponentielles.

Pour étudier la dynamique du front, nous avons effectué de nombreuses simulations grâce auxquelles nous avons pu mesurer la vitesse moyenne sur une longue période de temps, après dissipation de l'influence des conditions initiales. Ces simulations montrent que la vitesse asymptotique de l'épidémie dépend fortement du nombre d'individus par unité d'espace : une quantité d'hôte réduite diminue la vitesse du front. Ce phénomène peut s'expliquer par la stochasticité à l'avant du front, qui est d'autant plus forte que la population locale est petite. En adaptant les résultats de Brunet et Derrida [51], nous obtenons une approximation de la vitesse du front pour chacun des types w et m prenant en compte l'effet démographique de la taille de population finie :

$$c_i^{stoch} \approx c_i - \sqrt{\sigma r_i} \left(\frac{\pi}{\log\left(\frac{K_i}{h}\right)} \right)^2$$

où $i \in \{w, m\}$. Cette estimation est cohérente avec les résultats obtenus par simulation. En particulier, il existe une taille de population critique en-dessous de laquelle la vitesse du front n'est plus comparable à celle du mutant isolé : dans cette situation, le mutant ne peut pas envahir l'avant du front à cause de la taille trop petite de la population d'hôtes. La vitesse mesurée pour ces très petites populations est alors celle du résident. Quand nous augmentons la taille de la population, nous voyons apparaître une région dans laquelle la vitesse mesurée oscille entre celle du mutant et celle du résident. Pour les très grandes tailles de population nous retrouvons des résultats comparables avec ceux obtenus par notre modèle déterministe (1.19).

Discussion

Pour améliorer notre capacité à contrôler les maladies infectieuses, nous devons mieux appréhender l'effet conjoint des dynamiques épidémiologiques et évolutives des pathogènes. Notre compréhension théorique de l'évolution de la virulence est souvent fondée sur l'hypothèse que l'évolution intervient à une échelle de temps bien plus longue que celle de l'épidémiologie. Pourtant, ces deux échelles de temps peuvent se rencontrer dans de nombreuses situations à cause, par exemple, d'une grande variabilité génétique qui alimente la vitesse d'adaptation [132]. La théorie de l'épidémiologie évolutive nous donne alors des moyens de mieux comprendre la dynamique du pathogène au cours d'une épidémie, et précise dans quelle mesure l'épidémiologie interagit avec l'évolution.

Les validations empiriques et expérimentales de nos prédictions théoriques sont particulièrement difficiles car elles nécessitent un échantillonnage le long de la propagation d'une épidémie. Il existe pourtant des études de ce type, comme par exemple [155] qui suit l'infection par deux souches virales distinctes d'une colonie d'abeilles ; ou [167], qui suit l'évolution de populations de crapauds en Amérique Centrale, et analyse son déclin comme une observation indirecte de la propagation d'une épidémie. L'évolution expérimentale pourrait fournir un autre moyen de tester ces prédictions.

Yin [210], par exemple, a réalisé une expérience intéressante sur le phage T7, durant laquelle il a mesuré l'évolution du virus pendant sa propagation. A la différence des autres phages, T7 peut former des plaques qui grandissent indéfiniment dans des boîtes d'agar. Yin a observé l'apparition de mutants à l'avant du front, caractérisés par une plus grande fitness, ce qui confirme l'existence d'une différentiation génétique en fonction de la distance au front. Il n'est pas clair, cependant, que son étude rentre dans notre cadre théorique, mais une analyse plus poussée de ses résultats pourrait permettre de tester certaines de nos prédictions.

La théorie de l'évolution a montré que l'adaptation des espèces invasives peut dépendre de multiples traits d'histoire de vie. La constante de diffusion des hôtes σ, en particulier, est susceptible d'être sous une forte pression de sélection à l'avant du front de propagation [189]. D'autres cycles de vie pourraient être envisagés, dans lesquels cette constante de diffusion serait contrôlée par le pathogène, à la différence de notre modèle. Enfin, l'impact de différentes formes d'hétérogénéité en espace sur la propagation d'espèces a été étudiée dans [188]. Autoriser l'évolution du pathogène dans ces modèles permettrait d'étudier de nouveaux chemins adaptatifs dans lesquels les pathogènes pourraient se spécialiser sur certains hôtes ou, au contraire, adopter une stratégie plus généraliste. Dans ces environnements hétérogènes, une meilleure compréhension des dynamiques spatiales des pathogènes passe également par une analyse des interactions entre démographie, stochasticité et évolution à l'avant du front des épidémies.

1.3.3 Résumé du chapitre 4 : Fronts pulsatoires pour un système d'équations de Fisher-KPP hétérogènes en épidémiologie évolutive

Ce travail a été effectué en collaboration avec Matthieu Alfaro et a été soumis [7].

Dans ce chapitre nous étudions le système de réaction-diffusion

$$\begin{cases} u_t - u_{xx} = u\left(r_u(x) - \gamma_u(x)(u+v)\right) + \mu(x)(v-u) \\ v_t - v_{xx} = v\left(r_v(x) - \gamma_v(x)(u+v)\right) + \mu(x)(u-v), \end{cases} \tag{1.20}$$

où r_u et r_v sont des fonctions périodiques de période $L > 0$ et γ_u, γ_v et μ sont des fonctions positives et périodiques de période L. Le système (1.20) décrit la dynamique d'une population théorique divisée en deux génotypes u et v, vivant dans un habitat linéaire $x \in \mathbb{R}$. Nous supposons que chaque génotype induit un phénotype différent qui subit l'influence d'un environnement hétérogène. Les différences entre ces phénotypes s'expriment par une différence en terme de natalité, mortalité et capacité à soutenir la compétition pour une ressource finie, mais nous supposons que les constantes de diffusion de chacun des phénotypes restent similaires. Enfin, nous prenons en compte un processus de mutations entre chaque phénotype.

Les coefficients de réaction $r_u(x)$ et $r_v(x)$ représentent le taux d'accroissement de la population en l'absence de compétition, et prennent en considération les taux de naissance et de mort des individus. Nous autorisons ici r_u et r_v à prendre des valeurs négatives, correspondant à des zones très défavorables (taux de mort supérieur au taux de naissance). La fonction $\mu(x)$ correspond au taux de mutation entre les deux espèces. Nous supposons ici que le processus de mutation est symétrique, ce qui simplifie l'écriture du problème et les preuves du point de vue mathématique. Des résultats similaires pourraient sans doute être établis dans le cas de mutations non symétriques, bien que les preuvent puissent être plus techniques. Enfin, $\gamma_u(x)$ et $\gamma_v(x)$ représentent l'intensité de la compétition entre les deux phénotypes.

Ce cadre théorique est particulièrement bien adapté à la modélisation de la propagation des maladies infectieuses dans une population d'hôtes hétérogène. En effet, le système (1.20) peut être écrit comme limite d'un modèle microscopique [115], dans lequel on néglige l'influence des parasites sur la diffusion des hôtes.

Comme très souvent dans les équations de type KPP, le signe de la *valeur propre principale* du système linéarisé de (1.20) autour de 0 est crucial pour déterminer la survie en temps long de l'espèce. Rappelons que la valeur propre principale est l'unique réel λ_1 tel que le système linéaire :

$$-\varphi_{xx} = A(x)\varphi + \lambda_1\varphi, \quad x \in \mathbb{R}, \tag{1.21}$$

admet une solution classique $\varphi = \begin{pmatrix}\varphi_u\\ \varphi_v\end{pmatrix} > \begin{pmatrix}0\\0\end{pmatrix}$, où $A(x)$ est le champ de matrices

$$A(x) := \begin{pmatrix} r_u(x) - \mu(x) & \mu(x) \\ \mu(x) & r_v(x) - \mu(x)\end{pmatrix}.$$

Pour confirmer ce scénario, nous étudions d'abord l'existence d'un état stationnaire positif non trivial associé au problème (1.20), c'est-à-dire une solution périodique $(p(x) > 0, q(x) > 0)$ du système :

$$\begin{cases} -p_{xx} = (r_u(x) - \gamma_u(x)(p+q))p + \mu(x)(q-p) \\ -q_{xx} = (r_v(x) - \gamma_v(x)(p+q))q + \mu(x)(p-q). \end{cases}$$

Notre premier résultat est le suivant :

Théorème 1.3.4 (Sur les états stationnaires positifs)**.** *Si* $\lambda_1 > 0$ *alors* $(0,0)$ *est l'unique état stationnaire positif associé au problème* (1.20)*.*

En revanche, si $\lambda_1 < 0$ *alors il existe un état stationnaire non-trivial* $(p(x) > 0, q(x) > 0)$ *associé au problème* (1.20)*.*

Nous étudions ensuite le comportement en temps grand du problème de Cauchy associé au système (1.20). Nous montrons d'abord l'extinction lorsque la valeur propre principale λ_1 est strictement positive.

Proposition 1.3.5 (Extinction)**.** *Supposons $\lambda_1 > 0$. Soit $(u^0(x), v^0(x))$ un couple de fonctions positives et bornées. Alors, toute solution positive $(u(t,x), v(t,x))$ du problème de Cauchy associé à* (1.20) *partant de la condition initiale $(u^0(x), v^0(x))$ s'éteint exponentiellement vite :*

$$\max\left(\|u(t,\cdot)\|_{L^\infty(\mathbb{R})}, \|v(t,\cdot)\|_{L^\infty(\mathbb{R})}\right) = O(e^{-\lambda_1 t}).$$

La preuve est très simple car le système (1.20) est contrôlé supérieurement par le système linéarisé (i.e. sans compétition). Celui-ci étant coopératif, il admet un principe de comparaison. Le problème est nettement plus délicat lorque $\lambda_1 < 0$ puisqu'on ne peut pas s'affranchir de la compétition pour obtenir un contrôle inférieur. Pour montrer que la population envahit l'espace, nous allons construire des *fronts pulsatoires* pour le système (1.20).

Définition 1.3.6 (Front pulsatoire)**.** Un front pulsatoire pour le système (1.20) est une vitesse $c > 0$ et une solution positive classique $(u(t,x), v(t,x))$ du système (1.20), qui vérifie de plus

$$\begin{pmatrix} u\left(t+\frac{L}{c}, x\right) \\ v\left(t+\frac{L}{c}, x\right) \end{pmatrix} = \begin{pmatrix} u(t, x-L) \\ v(t, x-L) \end{pmatrix} \tag{1.22}$$

ainsi que les conditions aux limites :

$$\liminf_{t\to+\infty} \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \lim_{t\to-\infty} \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \tag{1.23}$$

localement uniformément en x.

À l'instar de [20], nous introduisons de nouvelles variables correspondant à un référentiel voyageant à vitesse c le long de l'axe des x, $(s, x) := (x - ct, x)$. Notre système se réécrit :

$$\begin{cases} -(u_{xx} + 2u_{xs} + u_{ss}) - cu_s = (r_u(x) - \gamma_u(x)(u+v))u + \mu(x)(v-u) \\ -(v_{xx} + 2v_{xs} + v_{ss}) - cv_s = (r_v(x) - \gamma_v(x)(u+v))v + \mu(x)(u-v) \end{cases} \tag{1.24}$$

et la contrainte (1.22) est alors équivalente à la L-périodicité en x des solutions du nouveau problème (1.24).

L'une des difficultés inhérentes à cette approche vient du fait que l'opérateur différentiel du membre de gauche dans (1.24) est elliptique dégénéré. Pour dépasser cette difficulté, nous construisons des solutions du problème régularisé :

$$\begin{cases} -u_{xx} - 2u_{xs} - (1+\varepsilon)u_{ss} - cu_s = (r_u(x) - \gamma_u(x)(u+v))u + \mu(x)(v-u) \\ -v_{xx} - 2v_{xs} - (1+\varepsilon)v_{ss} - cv_s = (r_v(x) - \gamma_v(x)(u+v))v + \mu(x)(u-v) \end{cases} \tag{1.25}$$

pour récupérer *a posteriori* des solutions au problème (1.24) lorsque $\varepsilon \to 0$. Cette technique de *viscosité évanescente* demande un soin particulier dans l'établissement d'estimations *a priori* qui ne dépendent pas de ε. Cette méthode a été utilisée par exemple dans [18, 20] pour des équations scalaires.

En plus de cette première difficulté, le système (1.20) n'admet pas de théorème de comparaison, contrairement aux études précédentes. Toutefois, si nous définissons les fronts pulsatoires dans un sens faible — voir (1.23) dans la définition 1.3.6 — nous pouvons alors construire des fronts pulsatoires pour l'équation (1.20) lorsque la valeur propre principale λ_1 est strictement négative. Ceci constitue le résultat principal de notre chapitre puisque, à notre connaissance, il s'agit de la première construction de fronts pulsatoires dans une situation de type KPP sans principe de comparaison (pour des constructions dans le cadre des nonlinéarités de type ignition, voir [59, 130]). Afin d'utiliser un argument topologique, il nous faut non seulement obtenir des estimations *a priori* dépendant finement de la régularisation ε, mais également prouver une généralisation aux systèmes elliptiques d'une estimation de type Bernstein sur les gradients [19].

Théorème 1.3.7 (Construction d'un front pulsatoire)**.** *Supposons $\lambda_1 < 0$. Alors, il existe un front pulsatoire solution de* (1.20)*, qui vérifie* (1.22) *et* (1.23)*.*

La vitesse c^* à laquelle voyage le front pulsatoire construit vérifie

$$0 < c^* \leq \bar{c}^0 := \inf\{c \geq 0 : \exists \lambda > 0, \mu_{c,0}(\lambda) = 0\}$$

où $\mu_{c,0}(\lambda)$ est la valeur propre de l'opérateur

$$S_{c,\lambda,0}\Psi := -\Psi_{xx} + 2\lambda\Psi_x + (\lambda(c-\lambda)Id - A(x))\Psi$$

avec conditions de bord L-périodiques. Nous conjecturons que $\bar{c}^0$ est effectivement la vitesse minimale des fronts pulastoires pour (1.20) — et donc la vitesse des fronts construits ici — comme c'est le cas dans pour les équations scalaires [203, 18, 20]. Cependant, ces preuves semblent s'appuyer fortement sur le fait que les fronts sont monotones, ce qui n'est pas attendu dans notre contexte sans comparaison.

1.3.4 Résumé du chapitre 5 : Fronts progressifs à valeur mesure pour une équation de réaction-diffusion non-locale

Ce chapitre fait l'objet d'un travail en fin de rédaction [113]. Il reste quelques passages à améliorer et l'introduction à écrire, mais tous les résultats et arguments mathématiques sont présents.

Dans ce chapitre nous nous intéressons à l'équation

$$u_t = u_{xx} + \mu(M \star u - u) + u(a(y) - K \star u) \tag{1.26}$$

où $u = u(t, x, y)$ représente une densité de population à un temps $t > 0$, une position spatiale $x \in \mathbb{R}$ et ayant pour trait phénotypique $y \in \Omega$, Ω étant un domaine borné régulier de $\mathbb{R}^n$. La fonction $a(y)$ représente la fitness du trait y, supposée indépendante du temps et de la position spatiale ; la fonction $K = K(y, z)$ est un noyau de compétition, qui correspond à l'intensité de la compétition entre le trait $y \in \overline{\Omega}$ et le trait $z \in \overline{\Omega}$; enfin, la fonction $M(y, z)$ modélise une probabilité de mutation du trait y vers le trait $z \in \overline{\Omega}$, qui intervient à un taux μ. Précisons enfin que, par $M \star u(t, x, y)$ et $K \star u(t, x, y)$, nous entendons $\int_\Omega M(y, z)u(t, x, z)dz$ et $\int_\Omega K(y, z)u(t, x, z)dz$, respectivement.

L'équation (1.26) est une généralisation naturelle du système étudié aux chapitres 2 et 3. D'une part, (1.26) peut être vue comme un système infini d'équations de réaction-diffusion semblables à (1.19), modélisant l'évolution d'une espèce possédant un grand nombre de traits phénotypiques différents. D'autre part, l'equation (1.26) est formellement équivalente au système (1.19) lorsque

$$\begin{aligned}
M(y, z) &= \frac{\mu_m}{\mu}\delta_{y=w} \otimes \delta_{z=m} + \frac{\mu_w}{\mu}\delta_{y=m} \otimes \delta_{z=w}, \quad \mu = \mu_w + \mu_m, \\
a(y) &= (r_w + \mu_m)\delta_{y=w} + (r_m + \mu_w)\delta_{y=m}, \\
K(y, z) &= \frac{r_w}{K_w}\delta_{y=w} \otimes (\delta_{z=w} + \delta_{z=m}) + \frac{r_m}{K_m}\delta_{y=m} \otimes (\delta_{z=w} + \delta_{z=m}),
\end{aligned}$$

où δ est la mesure de Dirac.

Nous nous intéressons plus particulièrement à la construction de fronts progressifs pour (1.26) lorsque les coefficients M, K et a sont des fonctions α-Hölder pour un $\alpha \in (0, 1)$. Pour cette équation, nous nous attendons à ce que les petites populations à l'avant du front déterminent la dynamique de propagation ; la solution u se comporte alors comme $u(t, x, y) \approx e^{-\lambda x}\varphi(y)$, où $\varphi(y)$ est une solution de l'équation linéarisée homogène associée à (1.26). Or ce problème linéaire n'admet pas toujours de solution continue : Coville [61], en particulier, donne une condition naturelle sur la fonction de fitness $a(y)$ et le taux de mutation μ, sous laquelle il n'existe pas de fonction propre φ continue au système linéarisé, mais seulement des mesures singulières. Nous sommes donc amenés à construire des fronts progressifs pour (1.26) dans un sens faible, tels que pour presque tout x, le front $u(t, x, \cdot)$ est une mesure sur $\overline{\Omega}$, sans espoir de régularité supplémentaire en général.

Précisons le type de fonctions pour lesquelles nous nous attendons à avoir des fronts singuliers pour (1.26). Il s'agit d'une condition sur le comportement local de a au voisinage de son maximum (comme remarqué dans [60, 61]).

Hypothèse 1.3.8 (Concentration). Nous disons que $a(y)$ vérifie l'hypothèse de *concentration* si

$$y \mapsto \frac{1}{\sup_{z\in\Omega} a(z) - a(y)} \in L^1(\Omega).$$

Notons, en particulier, qu'une fonction de fitness naturelle du type $a(y) = 1 - |y|^2$ satisfait l'hypothèse 1.3.8 dès que la dimension euclidienne de Ω est supérieure à 3.

Pour les équations de type KPP, la valeur propre principale de l'équation linéarisée joue un rôle central dans la détermination de la dynamique de (1.26). Ici, cette valeur propre n'est pas toujours associée à une fonction propre, comme rappelé plus haut. Nous reprenons donc la définition suivante.

Définition 1.3.9 (Valeur propre principale)**.** Nous appelons *valeur propre principale* associée à (1.26) la quantité

$$\lambda_1 := \sup\{\lambda, \exists \varphi \in C(\overline{\Omega}), \varphi > 0 \text{ telle que } \mu(M \star \varphi - \varphi) + \varphi(a(y) + \lambda) \leq 0\}. \tag{1.27}$$

Il est aisé de vérifier que cette définition a un sens et que $\lambda_1 \leq -(\sup a - \mu)$. Nous montrons une première proposition qui précise que, même dans le cas où λ_1 n'est pas associé à une fonction propre continue, λ_1 correspond à l'unique réel tel que le problème au valeurs propres a une solution faible.

Proposition 1.3.10 (Unicité de la valeur propre principale)**.** *Il existe un unique $\lambda \in \mathbb{R}$ tel que le problème*

$$\mu(M \star \varphi - \varphi) + (a(y) + \lambda)\varphi = 0 \tag{1.28}$$

admet une mesure positive non triviale comme solution, et $\lambda = \lambda_1$.

Si, de plus, $a(y)$ vérifie l'hypothèse 1.3.8, il existe un taux critique $\mu_0 > 0$ tel que si $0 < \mu < \mu_0$, alors

$$\lambda_1 = -(\sup a - \mu),$$

et dans ce cas, il existe une mesure φ solution de (1.28), dont la partie singulière est non nulle et concentrée sur $\Omega_0 := \{y \in \overline{\Omega}, a(y) = \sup a\}$.

Lorsque $\lambda_1 > 0$, nous pouvons montrer que toute solution au problème de Cauchy (1.26), partant d'une condition initiale positive et bornée, converge vers 0 en temps infini. Il suffit pour cela de construire une sur solution à l'équation linéarisée (dont u est sous solution) du type "exponentielle en temps fois un $\psi(y)$ continu et donné par (1.27)".

Dans ce travail nous nous concentrons sur le cas $\lambda_1 < 0$. Pour confirmer la survie en temps long de la population, nous montrons dans un premier temps l'existence d'un état stationnaire homogène $p = p(y)$, positif et non-trivial pour l'équation (1.26).

Théorème 1.3.11 (Survie)**.** *Supposons que $\lambda_1 < 0$. Il existe une solution faible, positive et non-triviale pour l'équation*

$$\mu(M \star p - p) + p(a(y) - K \star p) = 0, \tag{1.29}$$

c'est-à-dire une mesure positive $p \in M^1(\overline{\Omega})$ qui vérifie (1.29) *au sens faible, i.e.*

$$\forall \psi \in C(\overline{\Omega}), \quad \int_{\overline{\Omega}} \psi(y)\Big[\mu(M \star p)(y)dy + \big(a(y) - \mu - (K \star p)(y)\big)p(dy)\Big] = 0.$$

Sous l'hypothèse de concentration (Hypothèse 1.3.8), Bonnefon, Coville et Legendre [39] ont montré que (1.29) admet des solutions singulières pour μ assez petit et un noyau de compétition $K(y, z)$ indépendant du trait y. Leur construction exploite un argument de séparation des variables autorisé par l'hypothèse $K(y, z) = K(z)$. Ici, nous montrons que ce phénomène apparaît sous l'hypothèse plus générale que l'un des traits phénotypiques de fitness maximale (i.e. y_0 satisfaisant $a(y_0) = \sup a$) souffre moins de la compétition que tous les autres traits.

Hypothèse 1.3.12 (Concentration non-linéaire)**.** Dans le cadre de l'hypothèse 1.3.8, nous supposons de plus que pour un $y_0 \in \Omega_0 = \{y \in \overline{\Omega}, a(y) = \sup a\}$,

$$\forall (y, z) \in \overline{\Omega} \times \overline{\Omega}, K(y_0, z) \leq K(y, z).$$

Théorème 1.3.13 (Existence d'un état stationnaire singulier)**.** *Plaçons-nous dans le cadre de l'hypothèse 1.3.12, et supposons de plus $\lambda_1 < 0$. Il existe $\mu_0 > 0$ tel que pour tout $0 < \mu < \mu_0$, la mesure p construite au Théorème 1.3.11 a une singularité concentrée sur Ω_0.*

Nous introduisons maintenant notre notion de fronts progressifs, plus faible que la notion habituelle puisque nous nous attendons à construire des fronts potentiellement singuliers.

Définition 1.3.14 (Fronts progressifs)**.** Un *front progressif* pour (1.26) consiste en une vitesse $c \in \mathbb{R}$ et un noyau de transition u positif et défini sur $\mathbb{R} \times \overline{\Omega}$ (i.e. une mesure $u(dx, dy)$ s'écrivant $u(x, dy)dx$), qui satisfont

$$-cu_x - u_{xx} = \mu(M \star u - u) + u(a(y) - K \star u) \tag{1.30}$$

au sens des distributions. Nous demandons de plus les conditions aux limites :

$$\liminf_{\bar{x} \to +\infty} \int_{\mathbb{R} \times \overline{\Omega}} \psi(x + \bar{x}, y)u(dx, dy) > 0, \tag{1.31}$$

$$\limsup_{\bar{x} \to -\infty} \int_{\mathbb{R} \times \overline{\Omega}} \psi(x + \bar{x}, y)u(dx, dy) = 0, \tag{1.32}$$

pour toute fonction continue à support compact $\psi \in C_c(\mathbb{R} \times \overline{\Omega})$.

Notre résultat principal est le suivant.

Théorème 1.3.15 (Existence de fronts progressifs)**.** *Il existe un front progressif pour l'équation* (1.26)*, voyageant à la vitesse $c^* := 2\sqrt{-\lambda_1}$.*

Il semble difficile en général de déterminer si u a effectivement une partie singulière. Néanmoins, dans le cas où K est indépendant de la variable y, nous pouvons facilement construire des fronts singuliers grâce à un argument de séparation de variables. Plaçons-nous sous l'hypothèse 1.3.8 et choisissons un couple principal (λ_1, φ) où φ est une mesure singulière (un tel couple existe pour certains μ, d'après la Proposition 1.3.10). Quitte à multiplier φ par une constante positive, nous supposons $\int_{\overline{\Omega}} K(z)\varphi(dz) = 1$. Puisque $\lambda_1 < 0$, il existe un front positif connectant 0 en $+\infty$ à $-\lambda_1$ en $-\infty$, pour l'équation de Fisher-KPP

$$-\rho_{xx} - c\rho_x = \rho(-\lambda_1 - \rho),$$

dès que $c \geq c^* = 2\sqrt{-\lambda_1}$. Il est alors facile de vérifier que l'ansatz $u(x, dy) := \rho(x)\varphi(dy)$ satisfait la définition 1.3.14. De plus, par définition de φ, $u(x, \cdot)$ est singulière pour tout $x \in \mathbb{R}$.

1.4 Quelques perspectives

1.4.1 Déterminisme linéaire pour les systèmes de fronts pulsatoires

Nous nous intéressons à la conjecture $c^* = \overline{c}^0$ annoncée au chapitre 4 (voir Théorème 1.3.7 et discussion suivante) et, plus généralement, au *déterminisme linéaire* (au sens de Weinberger [203]) de la vitesse de propagation pour le système (1.20). Suivant une discussion fructueuse avec le Professeur Hiroshi Matano, une manière de montrer ce résultat serait d'étudier le système

$$\begin{cases} u_t - u_{xx} = u(r_u(x) - \gamma_u(x)(u+v) - \beta u) + \mu(x)(v-u) \\ v_t - v_{xx} = v(r_v(x) - \gamma_v(x)(u+v) - \beta v) + \mu(x)(u-v) \end{cases} \tag{1.33}$$

pour une constante $\beta > 0$ assez grande, contraignant ainsi u et v à rester "petits". En effet, dans ce cas, le système (1.33) est coopératif, et il est par ailleurs une sous-solution de (1.20). Enfin, le linéarisé en 0 de (1.33) est égal à celui de (1.20). Montrer le déterminisme linéaire pour le système (1.33), qui est coopératif, semble à portée de main, et fournirait l'estimation inférieure sur la vitesse qui complèterait la détermination de la vitesse pour (1.20).

L'idée d'augmenter l'auto-compétition des espèces pour récupérer des arguments de comparaison a été largement mise à profit dans le chapitre 5. Une résolution du problème de déterminisme linéaire pour les systèmes pulsatoires pourrait d'ailleurs se translater aux équations intégro-différentielles du type (1.26), ou en tout cas conduire à une meilleure compréhension de leur comportement.

Signalons une autre méthode qui pourrait potentiellement s'appliquer ici, utilisée par Girardin [109] dans le contexte des fronts progressifs pour les systèmes localement coopératifs en espace homogène. Il s'agit de construire des fronts sur-critiques (i.e. ayant une vitesse $c > \bar{c}^0$), grâce en particulier à une sous-solution construite comme différence de deux exponentielles, puis de prendre la limite $c \to \bar{c}^0$. Cette méthode — différente des constructions que nous avons largement utilisées ici — permettrait de construire directement des front ayant une vitesse $\bar{c}^0$, à condition néanmoins que les estimations puissent être reproduites dans le cas pulsatoire.

1.4.2 Apparition de multi-résistances en milieu hétérogène

Nous proposons d'étendre l'étude mathématique du chapitre 4 sur les systèmes de fronts pulsatoires à une application en épidémiologie évolutive. Nous envisageons le scénario suivant : une bactérie se propage dans une population d'hôtes, qui sont traités avec deux types d'antibiotiques A et B. Nous supposons que les hôtes traités par A et B sont regroupés en espace dans des zones distinctes, réparties selon un motif périodique. Enfin, trois phénotypes existent chez les pathogènes, un phénotype spécialiste dans la résistance à A, un autre spécialiste dans la résistance à B, et enfin un généraliste qui résiste moins bien que chacun des spécialistes dans un hôte traité par A ou B, mais mieux que le spécialiste pour A dans un hôte traité par B et que le spécialiste pour B dans un hôte traité par A. La dynamique en temps long (états stationnaires) d'un tel scénario a été étudiée par exemple dans [78, 77], où les auteurs concluent à l'existence d'une stratégie de traitement éliminant le pathogène multi-résistant (i.e. généraliste), ou à son cantonnement dans les zones de contact entre différents traitements.

Dans le cas d'une épidémie en cours de propagation (régime transitoire), en revanche, nous nous attendons à ce que le pathogène généraliste ait une vitesse moyenne de propagation supérieure à celles des spécialistes. Cela pourrait favoriser son apparition et son maintien à l'avant du front de propagation. Il serait intéressant d'établir des stratégies de traitement limitant la vitesse de propagation du pathogène, et de les mettre en relation avec les stratégies établies dans [78]. Pour cela, nous pourrions par exemple développer des formules asymptotiques en régimes fortement ou faiblement oscillants pour ce système, en s'inspirant des résultats de [79] et [121], respectivement. Des simulations numériques préliminaires montrent déjà l'apparition du multi-résistant à l'avant du front pour une vaste gamme de paramètres.

1.4.3 Étude du comportement des systèmes localement coopératifs pour d'autres formes d'hétérogénéités

L'hypothèse de travail employée dans le chapitre 4 (périodicité), qui a permis la prise en compte d'une hétérogénéité spatiale dans les systèmes de réaction-diffusion localement coopératifs, reste contraignante du point de vue des applications en biologie. Des généralisations de la vitesse de propagation existent pour des hétérogénéités plus complexes dans le contexte des équations scalaires, et ont été étudiées dans [24, 160], par exemple. Par degré de généralité croissant, il s'agirait de montrer des résultats semblables à ceux du chapitre 4 aux systèmes presque périodiques, strictement ergodiques, voire à coefficients aléatoires. Ces derniers sont particulièrement intéressants en vue d'applications en épidémiologie évolutive, pour lesquelles l'environnement est constitué d'hôtes dont les vulnérabilités et les résistances sont aléatoirement réparties dans l'environnement.

1.4.4 Singularité des fronts construits au chapitre 5

Dans le chapitre 5, nous construisons des fronts progressifs potentiellement singuliers pour une équation non-locale en trait. Rappelons qu'un exemple a été donné où le front, obtenu par séparation de variables grâce à une hypothèse sur le noyau de compétition, est effectivement singulier. En revanche, dans le cas général, la question de la singularité ou de la régularité des fronts construits n'a pas vraiment été envisagée pour le moment, et reste ouverte. Il serait intéressant d'exhiber des conditions sous lesquelles les fronts construits sont effectivement singuliers. Nous nous attendons à ce que le noyau de compétition K joue un rôle important dans ces phénomènes de concentration. Ainsi, sous l'hypothèse de concentration non linéaire 1.3.12, il s'agirait de connecter un état stationnaire singulier $p(y)$ (donné par le Théorème 1.3.13) à l'état instable 0. Formellement, ce front est voisin de $p(y)$ en $-\infty$, et de "exponentielle fois mesure propre en y" en $+\infty$, et ces deux états présentent l'avantage d'être concentrés dans Ω_0 (les points au maximum de fitness).

Chapitre 2

Existence and qualitative properties of travelling waves for an epidemiological model with mutations

2.1 Introduction

Epidemics of newly emerged pathogen can have catastrophic consequences. Among those who have infected humans, we can name the black plague, the Spanish flu, or more recently SARS, AIDS, bird flu or Ebola. Predicting the propagation of such epidemics is a great concern in public health. Evolutionary phenomena play an important role in the emergence of new epidemics: such epidemics typically start when the pathogen acquires the ability to reproduce in a new host, and to be transmitted within this new hosts population. Another phenotype that can often vary rapidly is the virulence of the pathogen, that is how much the parasite is affecting its host. Field data show that the virulence of newly emerged pathogens changes rapidly, which moreover seems related to unusual spatial dynamics observed in such populations ([128, 167], see also [148, 129]). It is unfortunately difficult to set up experiments with a controlled environment to study evolutionary epidemiology phenomena with a spatial structure, we refer to [15, 140] for current developments in this direction. Developing the theoretical approach for this type of problems is thus especially interesting. Notice finally that many current problems in evolutionary biology and ecology combine evolutionary phenomena and spatial dynamics: the effect of global changes on populations [162, 69], biological invasions [189, 136], cancers or infections [106, 94].

In the framework of evolutionary ecology, the virulence of a pathogen can be seen as a life-history trait [176, 92]. To explain and predict the evolution of virulence in a population of pathogens, many of the recent theories introduce a *trade-off* hypothesis, namely a link between the parasite's virulence and its ability to transmit from one host to another, see e.g. [8]. The basic idea behind this hypothesis is that the more a pathogen reproduces (in order to transmit some descendants to other hosts), the more it "exhausts" its host. A high virulence can indeed even lead to the premature death of the host, which the parasite within this host rarely survives. In other words, by increasing its transmission rate, a pathogen reduces its own life expectancy. There exists then an optimal virulence trade-off, that may depend on the ecological environment. An environment that changes in time (e.g. if the number of susceptible hosts is heterogeneous in time and/or space) can then lead to a Darwinian evolution of the pathogen population. For instance, in [30], an experiment shows how the composition of a viral population (composed of the phage λ and its virulent mutant λcl857, which differs from λ by a single locus mutation only) evolves in the early stages of the infection of an *E. coli* culture.

The Fisher-KPP equation is a classical model for epidemics, and more generally for biological invasions, when no evolutionary phenomenon is considered. It describes the time evolution of the density $n = n(t,x)$ of a population, where $t \geqslant 0$ is the time variable, and $x \in \mathbb{R}$ is a space variable. The model writes as follows:

$$\partial_t n(t,x) - \sigma \Delta n(t,x) = rn(t,x)\left(1 - \frac{n(t,x)}{K}\right). \tag{2.1}$$

It this model, the term $\sigma\Delta n(t,x) = \sigma\Delta_x n(t,x)$ models the random motion of the individuals in space, while the right part of the equation models the logistic growth of the population (see [196]): when the density of the population is low, there is little competition between individuals and the number of offsprings is then roughly proportional to the number of individuals, with a growth rate r ; when the density of the population increases, the individuals compete for e.g. food, or in our case for susceptible hosts, and the growth rate of the population decreases, and becomes negative once the population's density exceeds the so-called carrying capacity K. The model (2.1) was introduced in [89, 141], and the existence of travelling waves for this model, that is special solutions that describe the spatial propagation of the population, was proven in [141]. Since then, travelling waves have had important implications in biology and physics, and raise many challenging problems. We refer to [205] for an overview of this field of research.

In this study, we want to model an epidemic, but also take into account the possible diversity of the pathogen population. It has been recently noticed that models based on (2.1) can be used to study this type of problems (see [43, 5, 47]). Following the experiment [30] described above, we will consider two populations: a wild type population w, and a mutant population

m. For each time $t \geqslant 0$, $w(t,\cdot)$ and $m(t,\cdot)$ are the densities of the respective populations over a one dimensional habitat $x \in \mathbb{R}$. The two populations differ by their growth rate in the absence of competition (denoted by r in (2.1)) and their carrying capacity (denoted by K in (2.1)). We will assume that the mutant type is more virulent than the wild type, in the sense that it will have an increased growth rate in the absence of competition (larger r), at the expense of a reduced carrying capacity (smaller K). We assume that the dispersal rate of the pathogen (denoted by σ in (2.1)) is not affected by the mutations, and is then the same for the two types. Finally, when a parent gives birth to an offspring, a mutation occurs with a rate μ, and the offspring will then be of a different type. Up to a rescaling, the model is then:

$$\begin{cases} \partial_t w(t,x) - \Delta_x w(t,x) = w(t,x)\left(1-(w(t,x)+m(t,x))\right) \\ \qquad\qquad\qquad\qquad\qquad +\mu(m(t,x)-w(t,x)), \\ \partial_t m(t,x) - \Delta_x m(t,x) = rm(t,x)\left(1-\left(\frac{w(t,x)+m(t,x)}{K}\right)\right) \\ \qquad\qquad\qquad\qquad\qquad +\mu(w(t,x)-m(t,x)), \end{cases} \tag{2.2}$$

where $t \geq 0$ is the time variable, $x \in \mathbb{R}$ is a spatial variable, $r > 1$, $K < 1$ and $\mu > 0$ are constant coefficients. In (2.2), $r > 1$ represents the fact that the mutant population reproduces faster than the wild type population if many susceptible hosts are available, while $K < 1$ represents the fact that the wild type tends to out-compete the mutant if many hosts are infected. Our goal is to study the travelling wave solutions of (2.2), that is solutions with the following form :

$$w(t,x) = w(x-ct), \quad m(t,x) = m(x-ct),$$

with $c \in \mathbb{R}$. (2.2) can then be re-written as follows, with $x \in \mathbb{R}$:

$$\begin{cases} -cw'(x) - w''(x) = w(x)\left(1-(w(x)+m(x))\right) + \mu(m(x)-w(x)), \\ -cm'(x) - m''(x) = rm(x)\left(1-\left(\frac{w(x)+m(x)}{K}\right)\right) + \mu(w(x)-m(x)). \end{cases} \tag{2.3}$$

The existence of planar fronts in higher dimension ($x \in \mathbb{R}^N$) is actually equivalent to the $1D$ case ($x \in \mathbb{R}$), our analysis would then also be the first step towards the understanding of propagation phenomena for (2.2) in higher dimension.

There exists a large literature on travelling waves for systems of several interacting species. In some cases, the systems are monotonic (or can be transformed into a monotonic system). Then, sliding methods and comparison principles can be used, leading to methods close to the scalar case [197, 198, 178]. The combination of the inter-specific competition and the mutations prevents the use of this type of methods here. Other methods that have been used to study systems of interacting populations include phase plane methods (see e.g. [193, 86]) and singular perturbations (see [99, 98]). More recently, a different approach, based on a topological degree argument, has been developed for reaction-diffusion equations with non-local terms [25, 5]. The method we use here to prove the existence of travelling wave for (2.3) will indeed be derived from these methods. Notice finally that we consider here that dispersion, mutations and reproduction occur on the same time scale. This assumption is important from a biological point of view (and is satisfied in the particular λ phage epidemics that guides our study, see [30]). In particular, we will not use the Hamilton-Jacobi methods that have proven useful to study this kind of phenomena when different time scales are considered (see [153, 43, 47]).

This mathematical study has been done jointly with an article in biology work, see [115] (and Chapter 3). We then refer to this other article for a deeper analysis on the biological aspects of this work, as well as a discussion of the impact of stochasticity for a related individual-based model (based on simulations and heuristic arguments).

We will make the following assumption,

Assumption 2.1.1. $r \in (1, \infty)$, $\mu \in \left(0, \min\left(\frac{r}{2}, 1 - \frac{1}{r}, 1 - K, K\right)\right)$ and $K \in \left(0, \min\left(1, \frac{r}{r-1}\left(1 - \frac{\mu}{1-\mu}\right)\right)\right)$.

This assumption ensures the existence of a unique stationary solution of (2.2) of the form $(w, m)(t, x) \equiv (w^*, m^*) \in (0, 1) \times (0, K)$ (see Appendix 2.6.2). It does not seem very restrictive for biological applications, and we believe the first result of this study (Existence of travelling waves, Theorem 2.2.1) could be obtained under a weaker assumption, namely:

$$r \in (1, \infty), \quad K \in (0, 1), \quad \mu \in (0, K).$$

Throughout this document we will denote by f^w and f^m the terms on the left hand side of (2.3):

$$\begin{aligned} f^w(w, m) &:= w(1 - (w + m)) + \mu(m - w), \\ f^m(w, m) &:= rm\left(1 - \left(\frac{w+m}{K}\right)\right) + \mu(w - m). \end{aligned} \tag{2.4}$$

We organize our paper as follows : in Section 2.2, we will present the main results of this article, which are three fold: Theorem 2.2.1 shows the existence of travelling waves for (2.3), Theorem 2.2.2 describes the profile of the fronts previously constructed, and Theorem 2.2.3 relates the travelling waves for (2.3) to travelling waves of (2.1), when μ and K are small. sections 2.3, 2.4 and 2.5 are devoted to the proof of the three theorems stated in Section 2.2.

2.2 Main results

The first result is the existence of travelling waves of minimal speed for the model (2.2), and an explicit formula for this minimal speed. We recall that the minimal speed travelling waves are often the biologically relevant propagation fronts, for a population initially present in a bounded region only [48], and it seems to be the one that is relevant when small stochastic perturbations are added to the model [157]. Although we expect the existence of travelling waves for any speed higher than the minimal speed, we will not investigate this problem here — we refer to [25, 5] for the construction of such higher speed travelling waves for related models. Notice also that the convergence of the solutions to the parabolic model (2.2) towards travelling waves, and even the uniqueness of the travelling waves, remain open problems.

Theorem 2.2.1. *Let r, K, μ satisfy Assumption 2.1.1. There exists a solution $(c, w, m) \in \mathbb{R} \times C^\infty(\mathbb{R})^2$ of (2.3), such that*

$$\forall x \in \mathbb{R}, \quad w(x) \in (0,1),\, m(x) \in (0,K),$$

$$\liminf_{x\to-\infty}(w(x)+m(x)) > 0, \quad \lim_{x\to\infty}(w(x)+m(x)) = 0,$$

$$c = c_*,$$

where

$$c_* := \sqrt{2\left(1+r-2\mu+\sqrt{(r-1)^2+4\mu^2}\right)} \tag{2.5}$$

is the minimal speed $c > 0$ for which such a travelling wave exists.

The proof of Theorem 2.2.1 raises several difficulties:

- The system is not monotonic (see [193, 44]), which prevents the use of sliding methods to show the existence of traveling waves.
- The competition term has a negative sign, which means that comparison principles often cannot be used directly.

As mentioned in the introduction, new methods have been developed recently to show the existence of travelling wave in models with negative nonlocal terms (see [25, 5]). To prove Theorem 2.2.1, we take advantage of those recent progress by considering the competition term as a nonlocal term (over a set composed of only two elements : the wild and the virulent type viruses). The methods of [25, 5] are however based on the Harnack inequality (or related arguments), that are not as simple for systems of equations as they are for scalar equations (see [55]). We have thus introduced a different localized problem (see (2.13)), which allowed us to prove our result without any Harnack-type argument.

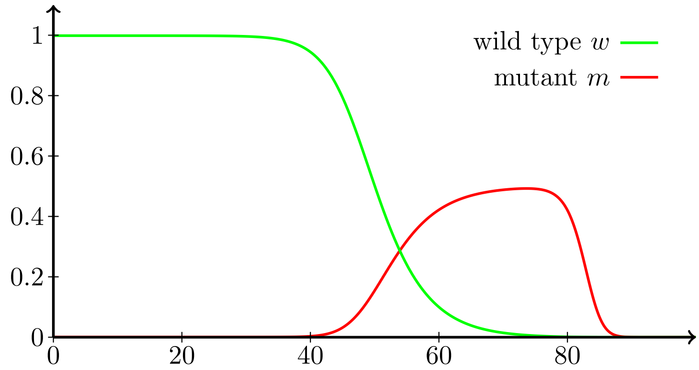


Figure 2.1 – Numerical simulation of (2.2) with $r = 2$, $K = 0.5$, $\mu = 0.01$, with a heaviside initial condition for w and null initial condition for m. The numerical code is based on an implicit Euler scheme. For large times, the solution seems to converge to a travelling wave, that we represent here, propagating towards large x. In the initial phase of the epidemics, the mutant (m, red line) population is dominant, but this mutant population is then quickly replaced by a population almost exclusively composed of wild types (w, green line). Although the steady states on the back of the wave seems to be close to $(w(x), m(x)) = (1, 0)$, we actually know that $(w^*, m^*) \in (0, 1) \times (0, K)$.

Our second result describes the shape of the travelling waves that we have constructed. We show that at most three different shapes are possible, depending on the parameters. In the most biologically relevant case, where the mutation rate is small, we show that the travelling wave constructed in Theorem 2.2.1 is as follows: the wild type density w is decreasing, while the mutant type density m has a unique global maximum, and is monotone away from this maximum. In numerical simulations of (2.2) (such as the one represented in Figure 2.1), we never observed a counterexample, even for large μ. This result also allows us to show that behind the epidemic front, the densities $w(x)$ and $m(x)$ of the two pathogens stabilize to w^*, m^*, which is the long-term equilibrium of the system if no spatial structure is considered. For some results on the monotonicity of solutions of the non-local Fisher-KPP equation, we refer to [84, 3]. For models closer to (2.2) (see e.g. [5, 43]), we do not believe any qualitative result describing the shape of the travelling waves exists.

Theorem 2.2.2. *Let r, K, μ satisfy Assumption 2.1.1. There exists a solution $(c, w, m) \in \mathbb{R}_+ \times C^\infty(\mathbb{R})^2$ of (2.3) such that*

$$\lim_{x\to-\infty}(w(x), m(x)) = (w^*, m^*), \quad \lim_{x\to\infty}(w(x), m(x)) = (0, 0),$$

where (w^*, m^*) is the unique solution of $f^w(w, m) = f^m(w, m) = 0$ in the *domain* $(0,1] \times (0,K]$.

The solution $(c,w,m) \in \mathbb{R}_+ \times C^\infty(\mathbb{R})^2$ *satisfies one of the three following properties:*

(a) *w is decreasing on $\mathbb{R}$, while m is increasing on $(-\infty,\bar{x}]$ and decreasing on $[\bar{x},\infty)$ for some $\bar{x} < 0$,*

(b) *m is decreasing on $\mathbb{R}$, while w is increasing on $(-\infty,\bar{x}]$ and decreasing on $[\bar{x},\infty)$ for some $\bar{x} < 0$,*

(c) *w and m are decreasing on $\mathbb{R}$.*

Moreover, there exists $\mu_0 = \mu_0(r,K) > 0$ such that if $\mu < \mu_0$, then there exists a solution as above which satisfies (a)*.*

Finally, we consider the special case where the mutant population is small (due to a small carrying capacity $K > 0$ of the mutant, and a mutation rate satisfying $0 < \mu < K$). If we neglect the mutants completely, the dynamics of the wild type would be described by the Fisher-KPP equation (2.1) (with $\sigma = r = K = 1$), and they would then propagate at the minimal propagation speed of the Fisher-KPP equation, that is $c = 2$. Thanks to Theorem 2.2.1, we already know that the mutant population will have a major impact on the minimal speed of the population, which becomes $c_* = 2\sqrt{r} + \mathcal{O}(\mu) > 2$, and thus shouldn't be neglected. In the next theorem, we show that the profile of w is indeed close to the travelling wave of the Fisher-KPP equation with the non-minimal speed $2\sqrt{r}$, provided the conditions mentioned above are satisfied (see Figure 2.2). The effect of the mutant is then essentially to speed up the epidemics.

Theorem 2.2.3. *Let $r \in (1,\infty)$, $K \in (0,1)$, $\mu \in (0,K)$ and $(c_*,w,m) \in \mathbb{R} \times C^0(\mathbb{R})^2$ (see Theorem 2.2.1 for the definition of c_*) be a positive solution of* (2.3) *such that*

$$\liminf_{x\to-\infty}(w(x)+m(x)) > 0, \quad \lim_{x\to\infty}(w(x)+m(x)) = 0.$$

There exists $C = C(r) > 0$, $\beta \in \left(0,\frac{1}{2}\right)$ and $\varepsilon > 0$ such that if $0 < \mu < K < \varepsilon$, then

$$\|w-u\|_{L^\infty} \leqslant CK^\beta,$$

where $u \in C^0(\mathbb{R})$ is a traveling wave of the Fisher-KPP equation, i.e. a solution (unique up to a translation) of

$$\begin{cases} -cu' - u'' = u(1-u), \\ \lim_{x\to-\infty} u(x) = 1, \ \lim_{x\to\infty} u(x) = 0, \end{cases} \tag{2.6}$$

with speed $c = c_0 = 2\sqrt{r}$.

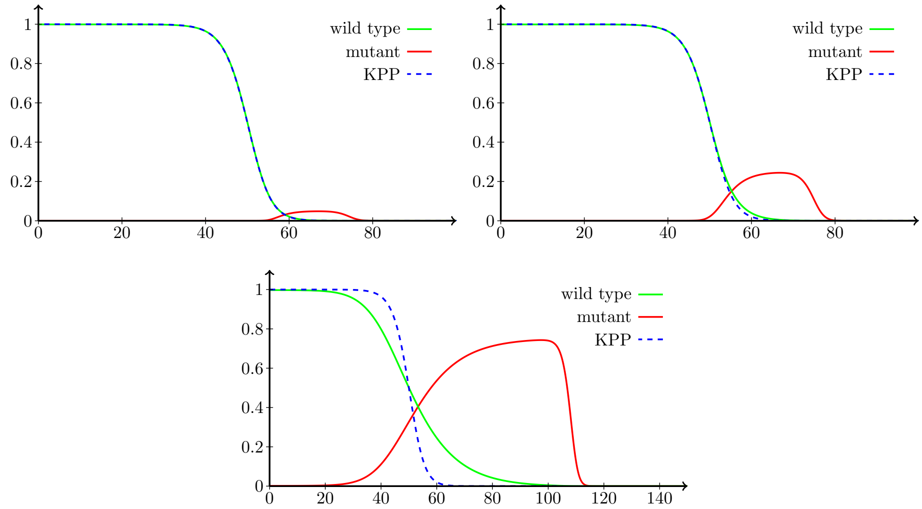


Figure 2.2 – Comparison of the travelling wave solutions of (2.2) and the travelling wave solution of the Fisher-KPP equation of (non-minimal) speed $2\sqrt{r}$. These figures are obtained for $r = 2$, $\mu = 0.001$, and three values of K: $K = 0.05, 0.25, 0.75$. We see that the agreement between the density of the wild type (w, green line) and the corresponding solution of the Fisher-KPP equation (u, dashed blue line) is good as soon as $K \leq 0.25$. The travelling waves solutions of (2.2) are obtained numerically as long-time solutions of (2.2) (based on an explicit Euler scheme), while the travelling waves solutions of the Fisher-KPP equations (for the given speed $2\sqrt{r}$ that is not the minimal travelling speed for the Fisher-KPP model) is obtained thanks to a phase-plane approach, with a classical ODE numerical solver.

Theorem 2.2.3 is interesting from an epidemiological point of view: it describes a situation where the spatial dynamics of a population would be driven by the characteristics of the mutants, even though the population of these mutant pathogens is very small, and thus difficult to sample in the field.

2.3 Proof of Theorem 2.2.1

We divide the proof of Theorem 2.2.1 in several steps. We refer to Remark 2.3.15 for the conclusion of the proof.

2.3.1 A priori estimates on a localized problem

We first consider a restriction of the problem (2.3) to a compact interval $[-a, a]$, for $a > 0$. More precisely, we consider, for $c \in \mathbb{R}$,

$$
\begin{cases}
w,\, m \in C^0([-a,a]), \\
-cw' - w'' = f^w(w,m)\chi_{w\geq 0}\chi_{m\geq 0}, \\
-cm' - m'' = f^m(w,m)\chi_{w\geq 0}\chi_{m\geq 0}, \\
w(-a) = w^*,\, m(-a) = m^*,\, w(a) = m(a) = 0,
\end{cases}
\tag{2.7}
$$

where f^w, f^m are defined in (2.4), and (w^*, m^*) is the stationary state solution to $f^w(w^*, m^*) = f^m(w^*, m^*) = 0$ (see Subsection 2.6.2).

Regularity estimates on solutions of (2.7)

The following result shows the regularity of the solutions of (2.7).

Proposition 2.3.1. *Let r, K, μ satisfy Assumption 2.1.1 and $a > 0$. If $w, m \in L^\infty([-a,a])$ satisfy*

$$
\begin{cases}
-cw' - w'' = f^w(w,m), \\
-cm' - m'' = f^m(w,m),
\end{cases}
\tag{2.8}
$$

on $[-a,a]$, where f^w, f^m are defined by (2.4)*, and $c \in \mathbb{R}$, then $w, m \in C^\infty([-a,a])$.*

Proof of Proposition 2.3.1. Since $f^w(w,m)$, $f^m(w,m) \in L^\infty([-a,a]) \subset L^p([-a,a])$ for any $p > 1$, the classical theory [108, Theorem 9.15] shows that the solutions of the Dirichlet problem associated with (2.8) are in $W^{2,p}$. This shows that $w, m \in W^{2,p}\big((-a,a)\big)$ for any $p > 1$. Then, thanks to the Sobolev imbeddings, we have $w, m \in C^{1,\alpha}\big((-a,a)\big)$ for any $0 \leqslant \alpha < 1$. It follows that $f(w,m)$ is a $C^{1,\alpha}\big((-a,a)\big)$ function of the variable $x \in (-a,a)$ (see (2.4) for the definition of f). Let us choose $\alpha \in (0,1)$. Now we can apply classical theory [108, Theorem 6.14] to deduce that $w, m \in C^{2,\alpha}\big((-a,a)\big)$. But then w'' and m'' verify a uniformly elliptic equation of the type

$$
-c(w'')' - (w'')'' = g,
$$

$$
-c(m'')' - (m'')'' = h,
$$

with $g, h \in C^{0,\alpha}\big((-a,a)\big)$, and we can apply again [108, Theorem 6.14]. This argument can be used recursively to show that $w, m \in C^{2n,\alpha}\big((-a,a)\big)$ for any $n \in \mathbb{N}$, so that finally, $w, m \in C^\infty\big((-a,a)\big)$. $\square$

Estimates solutions of (2.7)

In this subsection, we prove upper and lower estimates on solutions of (2.7).

Proposition 2.3.2. *Let r, K, μ satisfy Assumption 2.1.1, $a > 0$, and $c \in \mathbb{R}$. If $(w,m) \in C^0([-a,a])^2$ is a solution of* (2.7)*, then $w(x) > 0$ and $m(x) > 0$ for all $x \in [-a,a)$.*

Proof of Proposition 2.3.2. We observe that

$$f^w(w,m) = w(1-(w+m)) + \mu(m-w) = w(1-\mu-w) + m(\mu-w),$$

so that if $w \leqslant \min(\mu, 1-\mu)$, then $f^w(w,m)\chi_{w\geqslant 0}\chi_{m\geqslant 0} \geqslant 0$. Let $x_0 \in [-a,a]$ be such that $w(x_0) \leqslant 0$, and $[\alpha,\beta]$ be the maximal connected compound of the set $\{w \leqslant \min(\mu, 1-\mu)\}$ that contains x_0. Since $-cw' - w'' \geqslant 0$ over (α,β) and $w(\alpha), w(\beta) \geqslant 0$, the weak minimum principle imposes $\inf\limits_{(\alpha,\beta)} w \geqslant 0$, and thus $w(x_0) = 0$. But then w reaches its global minimum at x_0, so the strong maximum principle imposes that $x_0 \in \{\alpha, \beta\}$, or else w would be constant. We deduce then from our hypothesis $(w(-a) > 0, w(a) = 0)$ that $x_0 = \beta = a$. This shows that $w > 0$ in $[-a, a)$.

To show that $m > 0$, we notice that

$$\begin{aligned} f^m(w,m) &= rm\left(1 - \frac{w+m}{K}\right) + \mu(w-m) \\ &= m\left(r - \mu - \frac{r}{K}m\right) + w\left(\mu - \frac{r}{K}m\right), \end{aligned}$$

so that if $m \leqslant \min\left(\frac{K}{r}\mu, K\left(1-\frac{\mu}{r}\right)\right)$, then $f^m(w,m)\chi_{w\geqslant 0}\chi_{m\geqslant 0} \geqslant 0$. The end of the argument to show the positivity of w can the n be reproduced to show that $m > 0$. ☐

Proposition 2.3.3. *Let r, K, μ satisfy Assumption 2.1.1, $a > 0$, and $c \in \mathbb{R}$. If $(w,m) \in C^0([-a,a])^2$ is a positive solution of (2.7), then*

$$\forall x \in (-a,a), \quad w(x) < 1,$$

$$\forall x \in (-a,a), \quad m(x) < K.$$

Proof of Proposition 2.3.3. Let (w,m) be a positive solution of (2.7).

- Assume by contradiction that there exists $x_0 \in (-a,a)$ such that $w(x_0) > 1$. Let then $[a_1, a_2]$ be the maximal connected compound of the set $\{w \geqslant 1\}$ that contains x_0. Then in (a_1, a_2) we have

$$\begin{aligned} -cw' - w'' &= w(1-\mu-w-m) + \mu m \leqslant w(-\mu-m) + \mu m \\ &= m(\mu - w) - \mu w \leqslant 0, \end{aligned}$$

  along with $w(a_1) = w(a_2) = 1$, so that the weak maximum principle states $w \leqslant 1$ in (a_1, a_2), which is absurd because $w(x_0) > 1$. Therefore, $w(x) \leqslant 1$ for all $x \in (-a,a)$.

- Assume by contradiction that there exists $x_0 \in (-a, a)$ such that $m(x_0) > K$. Let then $[a_1, a_2]$ be the maximal connected compound of the set $\{m \geqslant K\}$ that contains x_0. Then in (a_1, a_2) we have

$$\begin{aligned} -cm' - m'' &= m\left(r - \mu - \frac{r}{K}(w+m)\right) + \mu w \\ &\leqslant m\left(-\mu - \frac{rw}{K}\right) + \mu w = w\left(\mu - \frac{r}{K}m\right) - \mu m \leqslant 0, \end{aligned}$$

thanks to Assumption 2.1.1. Since $m(a_1) = m(a_2) = K$, the weak maximum principle states $m \leqslant K$ in (a_1, a_2), which is absurd because $m(x_0) > K$. Therefore, $m(x) \leqslant K$ for all $x \in (-a, a)$.

- If $w(x) \in (\max(\mu, 1-\mu), 1]$, we still have the estimate

$$-cw'(x) - w''(x) \leqslant m(x)(\mu - w(x)) + w(x)(1 - \mu - w(x)) \leqslant 0.$$

If there exists $x_0 \in (-a, a)$ such that $w(x_0) = 1$, then w is locally equal to 1 thanks to the strong maximum principle. But in that case

$$0 = (-cw' - w'')(x_0) = -m(x_0) + \mu(m(x_0) - 1) < 0,$$

which is a contradiction. Hence, $w < 1$.

Similarly, if $m(x_0) = K$, we get

$$0 = (-cm' - m'')(x_0) = -K\mu + w(x_0)(\mu - r) < 0,$$

which is absurd, and thus $m < K$. □

Estimates on solutions of (2.7) when $c \geq c^*$ or $c = 0$

Next we show that the solutions of (2.7) degenerate when $a \to +\infty$ if the speed c is larger than the minimal speed c^* (see Theorem 2.2.1 for the definition of c^*).

Proposition 2.3.4 (Upper bound on c)**.** *Let r, K and μ satisfy Assumption 2.1.1. There exists $C > 0$ such that for $a > 0$ and $c \geqslant c_*$, any solution $(w, m) \in C^0([-a, a])^2$ of (2.7) satisfies*

$$\forall x \in [-a, a], \quad \max\left(w(x), m(x)\right) \leq Ce^{\frac{-c-\sqrt{c^2-c_*^2}}{2}(x+a)}.$$

Proof of Proposition 2.3.4. Let $c \geqslant c_*$, and

$$M := \begin{pmatrix} 1-\mu & \mu \\ \mu & r-\mu \end{pmatrix}.$$

Since $M + \mu\, Id$ is a positive matrix, the Perron-Frobenius theorem implies that M has a principal eigenvalue h^+ and a positive principal eigenvector X (that is $X_i > 0$ for $i = 1, 2$), given by

$$h_+ = \tfrac{1+r-2\mu+\sqrt{(1-r)^2+4\mu^2}}{2}, \quad X = \begin{pmatrix} 1 - r + \sqrt{(1-r)^2 + 4\mu^2} \\ 2\mu \end{pmatrix}. \tag{2.9}$$

Let $\psi_\eta(x) := \eta X e^{\lambda_- x}$ with $\lambda_- := \frac{-c-\sqrt{c^2-c_*^2}}{2}$ and $\eta > 0$. Then, we have

$$-c\psi_\eta' - \psi_\eta'' = M\psi_\eta = h_+\psi_\eta.$$

We define $\mathcal{A} = \{\eta, (\psi_\eta)_1 \geqslant w \text{ on } [-a, a]\} \cap \{\eta, (\psi_\eta)_2 \geqslant m \text{ on } [-a, a]\}$, which is a closed subset of $\mathbb{R}^+$. $\mathcal{A}$ is non-empty since w and m are bounded while $\left(Xe^{\lambda_- x}\right)_i \geq X_i e^{\lambda_- a} > 0$ for $i = 1, 2$.

Consider now $\eta_0 := \inf \mathcal{A}$. Then $(\psi_\eta)_1 \geq w$, $(\psi_\eta)_2 \geq m$, and there exists $x_0 \in [-a, a]$ such that either $(\psi_\eta)_1(x_0) = w(x_0)$ or $(\psi_\eta)_2(x_0) = m(x_0)$. We first consider the case where $(\psi_\eta)_1(x_0) = w(x_0)$. Then

$$-c(w - (\psi_\eta)_1)'(x_0) - (w - (\psi_\eta)_1)''(x_0) \leqslant -w(x_0)\,(w(x_0) + m(x_0)) \leqslant 0$$

over $[-a, a]$. The weak maximum principle [108, Theorem 8.1] implies that

$$\sup_{[-a,a]} (w - (\psi_\eta)_1) = \max((w - (\psi_\eta)_1)(-a), (w - (\psi_\eta)_1)(a)),$$

and then, thanks to the definition of η_0, $\sup_{[-a,a]} (w - (\psi_\eta)_1) = 0$. Since $w(a) = 0 < (\psi_\eta)_1(a)$, we have $(\psi_\eta)_1(-a) = w(-a)$, and thus

$$\eta_0 = \frac{b_w^-}{1 - r + \sqrt{(1-r)^2 + 4\mu^2}} e^{\lambda_- a}.$$

The argument is similar if $(\psi_\eta)_2(x_0) = m(x_0)$. This concludes the proof. $\square$

The following Proposition will be used to show that $c \neq 0$.

Proposition 2.3.5. *Let r, K, μ satisfy Assumption 2.1.1, and $a > a_0 := \frac{\pi}{\sqrt{2(1-\mu)}}$. Any positive solution $(w, m) \in C^0([-a, a])^2$ of (2.7) with $c = 0$ satisfies the estimate*

$$\max_{[-a_0,a_0]} (w + m) \geqslant \frac{K}{2}(1 - \mu). \tag{2.10}$$

Proof of Proposition 2.3.5. We assume that $c = 0$, $a > a_0$, and that (2.10) does not hold. We want to show that those assumptions lead to a contradiction. For $A \geqslant 0$, the function defined by

$$\psi_A(x) = A \cos\left(\sqrt{\frac{1-\mu}{2}} x\right),$$

is a solution of the equation $-\psi_A'' = \frac{1-\mu}{2}\psi_A$ over $[-a_0, a_0]$. Since $w, m > 0$ over $[-a_0, a_0]$ and are bounded, the set $\mathcal{A} := \{A, \forall x \in [-a_0, a_0], \psi_A(x) \leqslant \min(w(x), m(x))\}$ is a closed bounded nonempty set in $(0, +\infty)$. Let now $A_0 := \max \mathcal{A}$. We have $\psi_{A_0} \leqslant \min(w, m)$ over $[-a_0, a_0]$, and then, since (2.10) does not hold and $K < 1$,

$$\begin{aligned} -(w - \psi_{A_0})'' &\geqslant (1 - \max_{[-a_0,a_0]}(w+m) - \mu)w - \frac{1-\mu}{2}\psi_{A_0} \\ &\geqslant \frac{1-\mu}{2}(w - \psi_{A_0}) \geqslant 0. \end{aligned} \tag{2.11}$$

Similarly, using that $r > 1$,

$$-(m - \psi_{A_0})'' \geqslant \frac{1-\mu}{2}(m - \psi_{A_0}) \geqslant 0.$$

From the weak minimum principle [108, Theorem 8.1], we have

$$\begin{aligned} &\min\left(\inf_{[-a_0,a_0]}(w - \psi_{A_0}), \inf_{[-a_0,a_0]}(m - \psi_{A_0})\right) \\ &\quad = \min((w - \psi_{A_0})(-a_0), (w - \psi_{A_0})(a_0), (m - \psi_{A_0})(-a_0), (m - \psi_{A_0})(a_0)). \end{aligned}$$

But the left side of the equation is 0 by definition of A_0, while the right side is strictly positive since $\psi_{A_0}(-a_0) = \psi_{A_0}(a_0) = 0$. This proves Proposition 2.3.5 □

Remark 2.3.6. Notice that Propositions 2.3.1, 2.3.2, 2.3.3, 2.3.4 and 2.3.5 also holds if $(c, w, m) \in \mathbb{R} \times C^0([-a, a])$ is a solution of

$$\begin{cases} w,\, m \in C^0([-a, a]), \\ -cw' - w'' = (w(1 - (w + \sigma m)) + \mu(\sigma m - w))\, \chi_{w\geq 0}\chi_{m\geq 0}, \\ -cm' - m'' = \left(rm\left(1 - \left(\frac{\sigma w + m}{K}\right)\right) + \mu(\sigma w - m)\right) \chi_{w\geq 0}\chi_{m\geq 0}, \\ w(-a) = w^*,\, m(-a) = m^*,\, w(a) = m(a) = 0, \end{cases} \tag{2.12}$$

where $\sigma \in [0, 1]$. We notice also that Proposition 2.3.5 remains true if $(0, w, m) \in \mathbb{R} \times C^0([-a, a])$ is a solution of (2.12).

Finally, if $\sigma = 0$, Proposition 2.3.5 holds even if $c < 0$, thanks to the following argument: w and m are then the solutions of two uncoupled Fisher-KPP equations on $[-a, a]$, and w satisfies $-cw' - w'' \geq (1 - \mu)w\left(1 - \frac{w}{\min(\tilde{w}, 1-\mu)}\right)$. The maximum principle then shows that $w \geq \tilde{w}$ where $\tilde{w}$ is the solution of $-c\tilde{w}' - \tilde{w}'' = \tilde{w}\left(1 - \frac{\tilde{w}}{\min(w^*, 1-\mu)}\right)$ such that $\tilde{w}(-a) = \min(w^*, 1-\mu)$ and $\tilde{w}(a) = 0$. $\tilde{w}$ is monotonic (thanks to a sliding argument), and thus $c\tilde{w}' \geq 0$. The proof of Proposition 2.3.5, and in particular the estimate (2.11) can be reproduced for $\tilde{w}$. A similar method can be employed to estimate m.

2.3.2 Existence of solutions to a localized problem

To show the existence of travelling waves solutions of (2.3), we will follow the approach of [5]. The first step is to show the existence of solutions of (2.7) satisfying the additional normalization property $\max_{[-a_0,a_0]}(w+m) = \nu_0$, that is the existence of a solution (c, w, m) to

$$\begin{cases} (c,w,m) \in \mathbb{R} \times C^0([-a,a])^2, \\ -cw' - w'' = f^w(w,m)\chi_{w\geqslant 0}\chi_{m\geqslant 0}, \\ -cm' - m'' = f^m(w,m)\chi_{w\geqslant 0}\chi_{m\geqslant 0}, \\ w(-a) = w^*,\, m(-a) = m^*,\, w(a) = m(a) = 0, \\ \max_{[-a_0,a_0]}(w+m) = \nu_0, \end{cases} \tag{2.13}$$

where f^w, f^m are defined by (2.4), $\nu_0 = \min\left(\frac{K}{4}(1-\mu), \frac{w^*+m^*}{2}\right)$ and w^*, m^* are defined in the Appendix 2.6.2.

We introduce next the Banach space $(X, \|\cdot\|_X)$, with $X := \mathbb{R}\times C^0([-a,a])^2$ and $\|(c,w,m)\|_X := \max(|c|, \sup_{[-a,a]}|w|, \sup_{[-a,a]}|m|)$. We also define the operator

$$\begin{array}{cccc} K^\sigma: & X & \longrightarrow & X, \\ & (c,w,m) & \longmapsto & (c + \max_{[-a_0,a_0]}(\tilde{w}+\tilde{m}) - \nu_0, \tilde{w}, \tilde{m}) \end{array} \tag{2.14}$$

where $(\tilde{w},\tilde{m}) \in C^0([-a,a])^2$ is the unique solution of

$$\begin{cases} -c\tilde{w}' - \tilde{w}'' = \left[w(1-(w+\sigma m)) + \mu(\sigma m - w)\right]\chi_{w\geqslant 0}\chi_{m\geqslant 0} \text{ on } (-a,a), \\ -c\tilde{m}' - \tilde{m}'' = \left[rm\left(1 - \left(\frac{\sigma w+m}{K}\right)\right) + \mu(\sigma w - m)\right]\chi_{w\geqslant 0}\chi_{m\geqslant 0} \text{ on } (-a,a), \\ \tilde{w}(-a) = w^*,\, \tilde{m}(-a) = m^*,\, \tilde{w}(a) = \tilde{m}(a) = 0. \end{cases}$$

The solutions of (2.13) with $c \geqslant 0$ are then the fixed points of K^1 in the domain $\{(c,w,m), 0 \leqslant w \leqslant 1, 0 \leqslant m \leqslant K, c \geqslant 0\}$.

We define

$$\Omega := \big\{(c,w,m) \in \mathbb{R}_+ \times C^0([-a,a])^2;\ c \in (0,c_*),\ \forall x \in [-a,a], \\ -1 < w(x) < 1,\ -K < m(x) < K\big\},$$

where c_* is defined by (2.5).

Lemma 2.3.7. *Let r, K, μ satisfy Assumption 2.1.1, and $a > 0$. Then, $(K^\sigma)_{\sigma\in[0,1]}$, defined by (2.14), is a family of compact operators on $(X, \|\cdot\|_X)$, which is continuous with respect to $\sigma \in [0,1]$.*

Proof of Lemma 2.3.7. We can write $K^\sigma = (\mathcal{L}_D)^{-1} \circ \mathcal{F}^\sigma$ where $(\mathcal{L}_D)^{-1}$ is defined by

$$(\mathcal{L}_D)^{-1}(c,g,h) = (\tilde{c},\tilde{w},\tilde{m}),$$

where $(\tilde{c}, \tilde{w}, \tilde{m})$ is the unique solution of

$$\begin{cases} -c\tilde{w}' - \tilde{w}'' = g \text{ on } (-a,a), \\ -c\tilde{m}' - \tilde{m}'' = h \text{ on } (-a,a), \\ \tilde{w}(-a) = w^*,\ \tilde{m}(-a) = m^*, \\ \tilde{w}(a) = \tilde{m}(a) = 0, \\ \tilde{c} = c + \max\limits_{[-a_0,a_0]} (\tilde{w} + \tilde{m}) - \nu_0, \end{cases}$$

and $\mathcal{F}^\sigma$ is the mapping

$$\mathcal{F}^\sigma(c,w,m) = \Big(c, w(1-(w+\sigma m)) + \mu(\sigma m - w), \\ rm\left(1 - \frac{\sigma w + m}{K}\right) + \mu(\sigma w - m)\Big).$$

Then, $\sigma \mapsto \mathcal{F}^\sigma$ is a continuous mapping from $[0,1]$ to $C^0(\Omega, X)$, and $(\mathcal{L}_D)^{-1}$ is a continuous application from $(X, \|\cdot\|_X)$ into itself (see Lemma 2.6.2), it then follows that $\sigma \mapsto K^\sigma = (\mathcal{L}_D)^{-1} \circ \mathcal{F}^\sigma$ is a continuous mapping from $[0,1]$ to $C^0(\Omega, X)$. Finally, the operator $(\mathcal{L}_D)^{-1}$ is compact (see Lemma 2.6.2), which implies that K^σ is compact for any fixed $\sigma \in [0,1]$. □

We now introduce the following operator, for $\sigma \in [0,1]$:

$$F^\sigma := Id - K^\sigma. \tag{2.15}$$

Similarly, we introduce the operator

$$\begin{array}{rccc} K_\tau : & X & \longrightarrow & X, \\ & (c,w,m) & \longmapsto & (c + \max\limits_{[-a_0,a_0]} (\tilde{w} + \tilde{m}) - \nu_0, \tilde{w}, \tilde{m}) \end{array} \tag{2.16}$$

where $(\tilde{w}, \tilde{m}) \in C^0([-a,a])^2$ is the unique solution of

$$\begin{cases} -c\tilde{w}' - \tilde{w}'' = \tau w(1-\mu-w)\chi_{w\geqslant 0}\chi_{m\geqslant 0} \text{ on } (-a,a), \\ -c\tilde{m}' - \tilde{m}'' = \tau rm\left(1 - \frac{\mu}{r} - \frac{m}{K}\right)\chi_{w\geqslant 0}\chi_{m\geqslant 0} \text{ on } (-a,a), \\ \tilde{w}(-a) = w^*,\ \tilde{m}(-a) = m^*,\ \tilde{w}(a) = \tilde{m}(a) = 0. \end{cases} \tag{2.17}$$

The argument of Lemma 2.3.7 can be be reproduced to prove that $(K_\tau)_{\tau\in[0,1]}$ is also a continuous family of compact operators on $(X, \|\cdot\|_X)$, and we can define, for $\tau \in [0,1]$, the operator

$$F_\tau := Id - K_\tau. \tag{2.18}$$

Finally, we introduce, for some $\bar{c} < 0$ that we will define later on,

$$\tilde{\Omega} := \big\{(c,w,m) \in \mathbb{R}_+ \times C^0([-a,a])^2;\ c \in (\bar{c}, c_*),\ \forall x \in [-a,a], \\ -1 < w(x) < 1,\ -K < m(x) < K\big\}.$$

In the next Lemma, we show that the Leray-Schauder degree of F_0 in the domain $\tilde{\Omega}$ is non-zero as soon as $a > 0$ is large enough. We refer to [191, Chapter 12] or [50, Chapter 10 and 11] for more details on the Leray-Schauder degree.

Lemma 2.3.8. *Let r, K, μ satisfy Assumption 2.1.1. There exists $\bar{a} > 0$ such that the Leray-Schauder degree of F_0 in the domain $\tilde{\Omega}$ is non-zero for any $a \geqslant \bar{a}$.*

Proof of Lemma 2.3.8. We first notice that for $\tau = 0$, the solution $(\tilde{w}, \tilde{m})$ of (2.17) is independent of (w, m), and then,

$$F_0(c, w, m) = \left(\nu_0 - \max_{[-a_0,a_0]}(w_c + m_c), w - w_c, m - m_c\right),$$

where (w_c, m_c) is the solution of (2.17) with $\tau = 0$, i.e.

$$(w_c, m_c)(x) := \left(w^*\left(\frac{e^{-cx} - e^{-ca}}{e^{ca} - e^{-ca}}\right), m^*\left(\frac{e^{-cx} - e^{-ca}}{e^{ca} - e^{-ca}}\right)\right),$$

if $c \neq 0$, and $(w_c, m_c)(x) = (\frac{a-x}{2a}w^*, \frac{a-x}{2a}m^*)$ if $c = 0$. The solutions of $F_0(c, w, m) = 0$ then satisfy $w = w_c$ and $m = m_c$. In particular, the solutions of $F_0(c, w, m) = 0$ satisfy $0 < w < 1$ and $0 < m < K$ on $[-a, a)$, and then,

$$\begin{aligned}(c, w, m) \notin &\left\{(\tilde{c}, \tilde{w}, \tilde{m}) \in \mathbb{R} \times C^0([-a, a])^2;\ \exists x \in [-a, a],\ \tilde{w}(x) \in \{-1, 1\}\right\}\\ &\cup \left\{(\tilde{c}, \tilde{w}, \tilde{m}) \in \mathbb{R} \times C^0([-a, a])^2;\ \exists x \in [-a, a],\ \tilde{m}(x) \in \{-K, K\}\right\}.\end{aligned}$$

The solutions of $F_0(c_*, w, m) = 0$ also satisfy

$$\max_{[-a_0,a_0]}(w_{c_*} + m_{c_*}) \leq 2\frac{e^{c_* a_0}}{e^{c_* a} - 1},$$

so that $\max_{[-a_0,a_0]}(w_{c_*} + m_{c_*}) < \nu_0$ if $a > \bar{a}$ for some $\bar{a} > 0$. It follows that $F_0 = 0$ has no solution in $\overline{\tilde{\Omega}} \cap \left(\{c^*\} \times C^0([-a, a])^2\right)$, provided $a > \bar{a}$.

Finally, for $c \leq 0$, the solutions of $F_0(c, w, m) = 0$ satisfy $(w_c, m_c)(x) \geq (w_0, m_0)(x) = \left(-\frac{w^*}{2a}x + \frac{w^*}{2}, -\frac{m^*}{2a}x + \frac{m^*}{2}\right)$, so that

$$\max_{[-a_0,a_0]}(w_c + m_c) > \max_{[-a_0,a_0]}(w_0 + m_0) = \frac{w^* + m^*}{2}\left(1 + \frac{a_0}{a}\right) > \frac{w^* + m^*}{2} \geq \nu_0,$$

and $F_0 = 0$ has no solution in $\overline{\tilde{\Omega}} \cap \left(\mathbb{R}_- \times C^0([-a, a])^2\right)$.

Next, we notice that $c \mapsto \max_{[-a_0,a_0]}(w_c + m_c)$ is decreasing, and thus there exists a unique $c_0 \in (0, c_*)$ such that $\max_{[-a_0,a_0]}(w_{c_0} + m_{c_0}) = \nu_0$. We can then define

$$\Phi_\tau(c,w,m) = \left(\nu_0 - \max_{[-a_0,a_0]}(w_c+m_c), w-((1-\tau)w_c+\tau w_{c_0}),\right.$$
$$\left. m-((1-\tau)m_c+\tau m_{c_0})\right),$$

which connects continuously $F_0 = \Phi_0$ to

$$\Phi_1(c,w,m) = \left(\nu_0 - \max_{[-a_0,a_0]}(w_c+m_c), w-w_{c_0}, m-m_{c_0}\right).$$

Notice that $\Phi_\tau(c,w,m)=0$ implies $\max_{[-a_0,a_0]}(w_c+m_c)=\nu_0$, which in turn implies that $c=c_0$. For any $\tau\in[0,1]$, the only solution of $\Phi_\tau(c,w,m)=0$ is then $(c_0,w_{c_0},m_{c_0})\notin\partial\tilde\Omega$. Thus, the Leray-Schauder degree $\deg(F_0,\tilde\Omega)$ of F_0 is equal to $\deg(\Phi_1,\tilde\Omega)$. The latter can be explicitely computed since its variables are separated :

$$\begin{aligned}\deg(\Phi_1,\Omega) &= \deg\left(\nu_0 - \max_{[-a_0,a_0]}(w_c+m_c), (\bar c, c_*)\right)\\ &\quad\times\deg\left(w-w_{c_0}, \left\{\tilde w\in C^0([-a,a]),\ -1<\tilde w(x)<1\right\}\right)\\ &\quad\times\deg\left(m-m_{c_0}, \left\{\tilde m\in C^0([-a,a]),\ -K<\tilde m(x)<K\right\}\right)\\ &= 1.\end{aligned}$$

□

Next, we show that the Leray-Schauder degree of F^0 in the domain Ω is also non-zero, for $a>0$ is large enough.

Lemma 2.3.9. *Let r, K, μ satisfy Assumption 2.1.1. There exists $\bar a>0$ such that the Leray-Schauder degree of F^0 in the domain Ω is non-zero for any $a\geqslant\bar a$.*

Proof of Lemma 2.3.9. Thanks to Proposition 2.3.5 and Remark 2.3.6, any solution $(c,w,m)\in\tilde\Omega$ of (2.12) satisfies $c>0$, i.e. $(c,w,m)\in\Omega$. Thus,

$$\deg(F^0,\Omega)=\deg(F^0,\tilde\Omega)=\deg(F_1,\tilde\Omega). \tag{2.19}$$

For $\tau\in[0,1]$, any solution $(c,w,m)\in\tilde\Omega$ of $F_\tau(c,w,m)=0$ satisfies

$$-cw'-w''\geq-\mu w,\quad -cm'-m''\geq-\mu m.$$

Thus $w,m\geq\phi_c$, where ϕ_c is the solution of $-c\phi_c'-\phi_c''=-\mu\phi_c$ which satisfies $\phi_c(-a)=K$, $\phi_c(a)=0$. This solution can easily be computed explicitly, and satisfies (for any fixed $a>0$)

$$\lim_{c\to-\infty}\phi_c(0)=K.$$

We choose $-\bar{c} > 0$ large enough so that $\phi_{\bar{c}}(0) \geq \nu_0$ (notice that the constant $\bar{c} \in \mathbb{R}$ is not independent of a). Then, $F_\tau(\bar{c}, w, m) = 0$ implies $\max\limits_{[-a_0,a_0]}(w+m) \geq 2\phi_{\bar{c}}(0) > \nu_0$. Thus $F_\tau(c, w, m) = 0$ has no solution on $\left(\{\bar{c}\} \times C^0([-a,a])^2\right) \cap \overline{\tilde{\Omega}}$, for any $\tau \in [0,1]$. If $F_\tau(c,w,m) = 0$ with $(c,w,m) \in \overline{\tilde{\Omega}}$, applying the strong maximum principle shows that $0 < w < 1$ and $0 < m < K$ on $(-a,a)$ (notice that w and m are indeed solutions of two uncoupled Fisher-KPP equations on $[-a,a]$). Finally, since Proposition 2.3.4 applies to solutions of $F_\tau(c_*, w, m) = 0$, we have for any $\tau \in [0,1]$

$$\max_{[-a_0,a_0]}(w+m) \leq Ce^{-c_* \frac{a-a_0}{2}}.$$

Thus, $F_\tau(c,w,m) = 0$ has no solution on $\left(\{c_*\} \times C^0([-a,a])^2\right) \cap \overline{\tilde{\Omega}}$ if $a > 0$ is large enough (uniformly in $\tau \in [0,1]$).

We have shown that $F_\tau(c,w,m) = 0$ has no solution on $\partial\tilde{\Omega}$ for $\tau \in [0,1]$. Since $\tau \mapsto F_\tau$ is a continuous famlly of compact operators on $\tilde{\Omega}$, this implies that

$$\deg(F_1, \tilde{\Omega}) = \deg(F_0, \tilde{\Omega}),$$

which, combined to (2.19) and Proposition 2.3.8, concludes the proof. □

Proposition 2.3.10. *Let r, K, μ satisfy Assumption 2.1.1. There exists $\bar{a} > 0$ such that for $a \geqslant \bar{a}$, there exists a solution $(c,w,m) \in \mathbb{R} \times C^0([-a,a])^2$ of* (2.13) *with $c \in (0, c_*)$.*

Proof of Proposition 2.3.10. We first show that there exists no $(c,w,m) \in \partial\Omega$ satisfying $F^\sigma(c,w,m) = 0$ with $\sigma \in [0,1]$.

Assume by contradiction that such a solution exists. Then, Proposition 2.3.5 (see also Remark 2.3.6) implies that $c \neq 0$, and if $c = c_*$, then Proposition 2.3.4 (see also Remark 2.3.6) implies that

$$\max_{[-a_0,a_0]}(w+m) \leqslant Ce^{-c_* \frac{a-a_0}{2}}, \tag{2.20}$$

where $C > 0$ is a positive constant independent from $\sigma \in [0,1]$. If $a \geq a_0 + \frac{2}{c_*}\ln\left(\frac{2C}{\nu_0}\right)$, then $\max\limits_{[-a_0,a_0]}(w+m) \leq \frac{\nu_0}{2}$, which is a contradiction. Any solution $(c,w,m) \in \overline{\Omega}$ of $F^\sigma(c,w,m) = 0$ then satisfies $c \in (0, c_*)$, as soon as $a > 0$ is large enough.

Then, we remark that any solution $(c,w,m) \in \overline{\Omega}$ of $F^\sigma(c,w,m) = 0$ is a solution of (2.12). Proposition 2.3.2 and Proposition 2.3.3 (see also Remark 2.3.6) then imply that for any $x \in (-a,a)$, $0 < w(x) < 1$ and $0 < m(x) < K$.

We have shown that $F^\sigma(c,w,m) = 0$ had no solution $(c,w,m) \in \partial\Omega$, for $\sigma \in [0,1]$. Finally, $(F_\sigma)_{\sigma\in[0,1]}$ is a continuous family of compact operators (see Lemma 2.3.7) and thus $\deg(F^\sigma, \Omega)$ is independent of $\sigma \in [0,1]$. In particular, thanks to Lemma 2.3.9, if $a > 0$ is large enough,

$$\deg(F^1, \Omega) = \deg(F^0, \Omega) \neq 0.$$

This shows that there exists a solution $(c, w, m) \in \Omega$ of $F^1(c, w, m) = 0$, i.e. a solution (c, w, m) of (2.13) in Ω. This finishes the proof of Proposition 2.3.10. □

2.3.3 Construction of a travelling wave

Proposition 2.3.11. *Let r, K, μ satisfy Assumption 2.1.1. There exists a solution $(c, w, m) \in (0, c_*] \times C^0(\mathbb{R})^2$ of problem (2.3), which satisfies $0 < w(x) < 1$ and $0 < m(x) < K$ for $x \in \mathbb{R}$, as well as $(w + m)(0) = \nu_0$.*

Proof of Proposition 2.3.11. For $n \geq 0$, let $a_n := \bar{a} + n$ (where $\bar{a} > 0$ is defined in Proposition 2.3.10), and (c_n, w_n, m_n) be a solution of (2.13) (which exists thanks to Proposition 2.3.10). We denote by (w_n^k, m_n^k) the restriction of (w_n, m_n) to $[-a_k, a_k]$ $(k < n)$. From interior elliptic estimates [108, Theorem 8.32], there exists a constant $C > 0$ independent of $k > 0$, such that for any $n \geq k + 1$,

$$\max\left(\left\| w_n|_{[-a_k,a_k]} \right\|_{C^1([-a_k,a_k])}, \left\| m_n|_{[-a_k,a_k]} \right\|_{C^1([-a_k,a_k])} \right) \leqslant C,$$

Since $c_n \in [0, c^*]$ for all $n \in \mathbb{N}$, we can extract from (c_n, w_n, m_n) a subsequence (that we also denote by (c_n, w_n, m_n)), such that $c_n \to c_0$ for some $c_0 \in [0, c^*]$. Since $c_n \in (0, c_*)$ for all $n \geq 3$, the limit speed satisfies $c_0 \in [0, c_*]$. Thanks to the Arzelà-Ascoli Theorem, $C^1([-a_k, a_k])$ is compactly imbedded in $C^0([-a_k, a_k])$. We can then use a diagonal extraction, to get a subsequence such that w_n and m_n both converge uniformly on any compact interval of $\mathbb{R}$. Let w_0, $m_0 \in C^0(\mathbb{R})$ the limits of (w_n) and (m_n) respectively. Then, thanks to the uniform convergence, we have

$$\forall x \in \mathbb{R}, \quad 0 \leqslant w_0(x) \leqslant 1, \quad 0 \leqslant m_0(x) \leqslant K,$$

and

$$-c_0 w_0' - w_0'' = f^w(w_0, m_0) \text{ on } \mathbb{R},$$
$$-c_0 m_0' - m_0'' = f^m(w_0, m_0) \text{ on } \mathbb{R},$$

in the sense of distributions. Thanks to Proposition 2.3.1, these functions are a classical solutions of (2.3). Moreover, we have $\max\limits_{[-a_0,a_0]}(w_0 + m_0) = \nu_0$, and Lemma 2.3.5 implies that $c_0 \neq 0$. Finally, up to a shift, $w_0(0) + m_0(0) = \nu_0$. □

In the next proposition, we show that the solution of (2.3) obtained in Proposition 2.3.11 are indeed propagation fronts.

Proposition 2.3.12. *Let r, K, μ satisfy Assumption 2.1.1 and $(c, w, m) \in \mathbb{R} \times C^0(\mathbb{R})^2$ a solution of (2.3) such that $(w+m)(0) = \nu_0$. Then $w+m$ is decreasing on $(0, +\infty)$,*

$$\lim_{x\to\infty} w(x) = \lim_{x\to\infty} m(x) = 0,$$

and $w(x) + m(x) \geq \nu_0$ on $(-\infty, 0]$.

Proof of Proposition 2.3.12. Assume that $w(x)+m(x) < K$, and assume by contradiction that $w'(x) + m'(x) \geq 0$. Then,

$$\begin{aligned} -c(w+m)'(x) - (w+m)''(x) &= w(x)(1 - (w(x) + m(x))) \\ &\quad + rm(x)\left(1 - \frac{w(x)+m(x)}{K}\right), \end{aligned} \tag{2.21}$$

where the right side positive, which shows $(w+m)''(x) < 0$.

If there exists $x_0 \in \mathbb{R}$ satisfying $w(x_0) + m(x_0) < K$, and $w'(x_0) + m'(x_0) \geq 0$, then we can define $\mathcal{C} = \{x \leqslant x_0, \forall y \in [x, x_0], (w+m)''(y) \leqslant 0\}$. Then $\mathcal{C} \neq \varnothing$ and $\mathcal{C}$ is closed since $(w+m)''$ is continuous. Let $x_1 \in \mathcal{C}$. Then $(w+m)'$ is decreasing on $[x_1, x_0]$, so that $(w+m)'(x_1) \geqslant (w+m)'(x_0) > 0$ and $(w+m)(x_1) \leqslant (w+m)(x_0)$. (2.21) then implies that $(w+m)''(x_1) < 0$, which proves that $\mathcal{C}$ is open, and thus $\mathcal{C} = (-\infty, 0)$. This implies in particular that $w(x) + m(x) < 0$ for some $x < x_0$, which is a contradiction. We have then proven that $x \mapsto w(x) + m(x)$ is decreasing on $[x_0, \infty)$ as soon as $w(x_0) + m(x_0) \leq K$.

Since (w, m) is given by Proposition 2.3.11, we have $(w+m)(0) = \nu_0 \leq K$ and thus $w(x) + m(x) \geq \nu_0$ for $x \leq 0$. Moreover, $x \mapsto w(x) + m(x)$ is decreasing on $[0, \infty)$.

Then, $\lim_{x\to\infty} w(x) + m(x) = l \in [0, K)$ (the limit exists since $w+m$ is decreasing near $+\infty$). Thus $\lim_{x\to\infty} w'(x) + m'(x) = \lim_{x\to\infty} w''(x) + m''(x) = 0$, since w and m are regular. Finally

$$\lim_{x\to\infty} \left(-c(w+m)'(x) - (w+m)''(x)\right) = 0,$$

which, combined to (2.21), proves that $\lim_{x\to\infty} w(x) + m(x) = 0$. ☐

2.3.4 Characterization of the speed of the constructed travelling wave

Lemma 2.3.13. *Let r, K, μ satisfy Assumption 2.1.1 and $(c, w, m) \in \mathbb{R} \times C^0(\mathbb{R})^2$ be a solution of (2.3) such that $(w+m)(0) = \nu_0$. Then, there exists $x_0 \in \mathbb{R}$ and $C > 0$ such that*

$$\forall x \geqslant x_0, \quad w(x) + m(x) \leqslant C \min(w(x), m(x)).$$

Proof of Lemma 2.3.13. Let $S(x) := w(x) + m(x)$, and $\alpha > 0$. Then

$$- c(S - \alpha w)' - (S - \alpha w)'' = ((1 - S) - (1 - S - \mu)\alpha)w + (S - w)\left(r\left(1 - \frac{S}{K}\right) - \alpha\mu\right).$$

Let $x_1 \in \mathbb{R}$ such that $S(x) \leqslant \frac{1-\mu}{2}$ for all $x \geq x_1$ (x_1 exists thanks to Proposition 2.3.12). Then, for $\alpha \geqslant \alpha_0 := \max\left(\frac{2}{1-\mu}, \frac{r}{\mu}\right)$ and $x \geqslant x_1$,

$$-c(S - \alpha w)'(x) - (S - \alpha w)''(x) \leqslant 0.$$

Let $\alpha_1 := \max\left(\frac{S(x_1)}{w(x_1)}, \alpha_0\right) + 1$. Then $-c(S - \alpha_1 w)' - (S - \alpha_1 w)'' \leqslant 0$ over $(x_1, +\infty)$. We can then apply the weak maximum principle to show that for any $x_2 > x_1$,

$$\max_{[x_1,x_2]} (S - \alpha_1 w)(x) = \max\left((S - \alpha_1 w)(x_1), (S - \alpha_1 w)(x_2)\right).$$

Since $(S - \alpha_1 w)(x_1) \leqslant 0$ and $\lim\limits_{x_2 \to +\infty} (S - \alpha_1 w)(x_2) = 0$, we have indeed shown that $\sup_{[x_1,\infty)} (S - \alpha_1 w)(x) = 0$, and then,

$$\forall x \geq x_1, \quad w(x) + m(x) \leq \alpha_1 w(x).$$

A similar argument can be used to show that there exists $x_2 \in \mathbb{R}$ and $\alpha_2 > 0$ such that $w(x) + m(x) \leqslant \alpha_2 m(x)$ for $x \geqslant x_2$, which concludes the proof of the Lemma. ☐

Proposition 2.3.14. *Let r, K, μ satisfy Assumption 2.1.1 and $(c, w, m) \in \mathbb{R}_+ \times C^0(\mathbb{R})^2$ a solution of (2.3) such that $(w + m)(0) = \nu_0$ and $c \leq c_*$. Then, $c = c_*$.*

Remark 2.3.15. Combined to Proposition 2.3.11 and Proposition 2.3.12, this proposition completes the proof of Theorem 2.2.1.

Proof of Proposition 2.3.14. Let $(c, w, m) \in [0, c_*] \times C^0(\mathbb{R})^2$ a solution of (2.3) such that $(w + m)(0) = \nu_0$. Thanks to Lemma 2.3.13, there exists $x_0 > 0$ and $C > 0$ such that

$$\begin{cases} -cw' - w'' \geq w(1 - \mu - Cw) + \mu m, \\ -cm' - m'' \geq m(r - \mu - Cm) + \mu w. \end{cases}$$

Let now $\varphi_\eta(x + x_1) := \eta e^{-\frac{c}{2}x} \sin\left(\frac{\sqrt{4h-c^2}}{2}x\right)$, where $\eta > 0$, $h \geq c^2/4$ and $x_1 > x_0$. φ_η then satisfies $\varphi_\eta(x_1) = \varphi_\eta\left(x_1 + 2\pi/\sqrt{4h - c^2}\right) = 0$, and

$-c\varphi_\eta' - \varphi_\eta'' = h\varphi_\eta$ on $\left[x_1, x_1 + 2\pi/\sqrt{4h-c^2}\right]$. $\psi_\eta := \varphi_\eta X$ (X is defined by (2.9)) is then a solution of

$$-c\psi_\eta' - \psi_\eta'' = (M + (h - h_+)Id)\psi_\eta,$$

where h_+ is defined by (2.9), and we can also write this equality as follows

$$\begin{cases} -c(\psi_\eta)_1' - (\psi_\eta)_1'' = (\psi_\eta)_1\left(1 - \mu + (h - h_+)\right) + \mu(\psi_\eta)_2, \\ -c(\psi_\eta)_2' - (\psi_\eta)_2'' = (\psi_\eta)_2\left(r - \mu + (h - h_+)\right) + \mu(\psi_\eta)_1. \end{cases}$$

Assume now that $c < c_*$. Then, we can choose $c^2/4 < h < c_*^2/4 = h_+$, and define

$$\bar\eta = \max\Big\{\eta > 0;\ \forall x \in \left[x_1, x_1 + 2\pi/\sqrt{4h-c^2}\right],\ (\psi_\eta)_1(x) \leq w(x), \\ (\psi_\eta)_2(x) \leq m(x)\Big\}.$$

Since w and m are positive bounded function, $\bar\eta > 0$ exists, and since

$$(\psi_\eta)_i(x_1) = (\psi_\eta)_i\left(x_1 + 2\pi/\sqrt{4h-c^2}\right) = 0,$$

there exists $\bar x \in \left(x_1, x_1 + 2\pi/\sqrt{4h-c^2}\right)$ such that either $(\psi_\eta)_1(\bar x) = w(\bar x)$ or $(\psi_\eta)_2(\bar x) = m(\bar x)$. Assume w.l.o.g. that $(\psi_\eta)_1(\bar x) = w(\bar x)$. Then $w - (\psi_\eta)_1$ has a local minimum in $\bar x$, which implies that

$$\begin{aligned} 0 \geq & - c(w - (\psi_{\bar\eta})_1)'(\bar x) - (w - (\psi_{\bar\eta})_1)''(\bar x) \\ \geq & \left[w(\bar x)(1 - \mu - Cw(\bar x)) + \mu m(\bar x)\right] - \Big[(\psi_{\bar\eta})_1(\bar x)\left(1 - \mu + (h - h_+)\right) \\ & + \mu(\psi_{\bar\eta})_2(\bar x)\Big] \\ \geq & (\psi_{\bar\eta})_1(\bar x)\left[(h_+ - h) - C(\psi_{\bar\eta})_1(\bar x)\right], \end{aligned}$$

and then $\bar\eta \geq (h_+ - h)/(CX_1)$. A similar argument holds if $(\psi_\eta)_2(\bar x) = m(\bar x)$, so that in any case, $\bar\eta \geq (h_+ - h)/(C\max(X_1, X_2))$, and $\psi_{\bar\eta}(x_1 + \cdot) \leq m$, $\psi_{\bar\eta}(x_1 + \cdot) \leq m$ on $\left[x_1, x_1 + 2\pi/\sqrt{4h-c^2}\right]$, as soon as $x_1 \geq x_0$. In particular, for any $x_1 \geq x_0$,

$$w\left(x_1 + \pi/\sqrt{4h-c^2}\right) \geq \frac{h_+ - h}{C\max(X_1, X_2)} e^{-\frac{c\pi}{2\sqrt{4h-c^2}}} X_1 > 0,$$

which is a contradiction, since $w(x) \to_{x\to\infty} 0$ thanks to Proposition 2.3.12.
$\square$

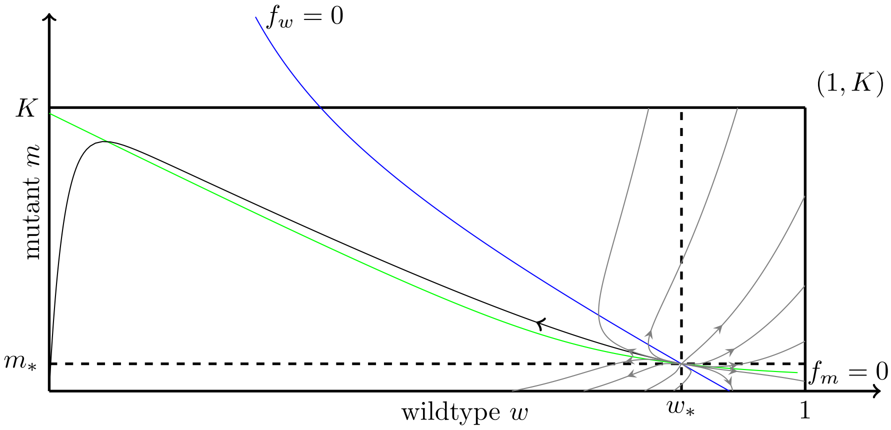


Figure 2.3 – Phase-plane-type representation of a solution of (2.7): we represent (dark line) $x \mapsto (w(x), m(x)) \in [0,1] \times [0,K]$. Note that the usual phase-plane for (2.7) is of dimension 4. The blue line represents the set of (w,m) such that $f^w(w,m) = 0$ (see (2.4)), $f^w(w,m) > 0$ for (m,w) on the left of the blue curve. The green line represents the set of (w,m) such that $f^m(w,m) = 0$ (see (2.4)), $f^m(w,m) > 0$ for (m,w) under the green curve. The gray lines represent several other solutions of (2.3) such $(w(-a), m(-a)) = (w^*, m^*)$. The dashed dark lines separate this phase plane into four compartiments that will be used in the third step of the proof of Lemma 2.4.1. Finally, the solid black line corresponds to the travelling wave.

2.4 Proof of Theorem 2.2.2

2.4.1 General case

The proof of the next lemma is based on a phase-plane-type analysis, see Figure 2.3

Lemma 2.4.1. *Let r, K, μ satisfy Assumption 2.1.1. Let $(c, w, m) \in \mathbb{R}_+ \times C^0([-a,a])^2$ be a solution of* (2.7)*. Then there exists $\bar{x} \in [-a, 0)$ such that one of the following properties is satisfied:*

- *w is decreasing on $[-a, a]$, while m is increasing on $[-a, \bar{x}]$ and decreasing on $[\bar{x}, a]$,*
- *m is decreasing on $[-a, a]$, while w is increasing on $[-a, \bar{x}]$ and decreasing on $[\bar{x}, a]$.*

Proof of Lemma 2.4.1. Step 1: sign of f^w and f^m.

We recall the definition (2.4) of f^w, f^m. The inequality $f^w(w,m) \geq 0$ is equivalent, for $w \in [0,1]$ and $m \in [0,K]$, to

$$w \leq \phi_w(m) := \frac{1}{2}\left[1 - \mu - m + \sqrt{(1-\mu-m)^2 + 4\mu m}\right]. \tag{2.22}$$

Notice that $m \in [0, K] \mapsto \phi_w(m)$ is a decreasing function (see Lemma 2.6.3), that divides the square $\{(w, m) \in [0, 1] \times [0, K]\}$ into two parts.

Similarly, $f^m(w, m) \geq 0$ is equivalent, for $w \in [0, 1]$ and $m \in [0, K]$, to

$$m \leq \phi_m(w) := \frac{1}{2}\left[K - \frac{\mu K}{r} - w + \sqrt{\left(K - \frac{\mu K}{r} - w\right)^2 + 4\frac{\mu K}{r} w}\right]. \tag{2.23}$$

Here also, $w \in [0, 1] \mapsto \phi_m(w)$ is a decreasing function (see Lemma 2.6.3), since $\mu \leq 1/2$ (see Assumption 2.1.1), that divides the square $\{(w, m) \in [0, 1] \times [0, K]\}$ into two parts.

Step 2: possible monotony changes of $w(x)$, $m(x)$. Let $(c, w, m) \in \mathbb{R}_+ \times C^0([-a, a])^2$ be a solution of (2.7). If $w'(x) \geq 0$ for some $x > -a$, we can define $\bar{x} := \inf\{y \geq x;\, w'(y) < 0\}$. Then $w'(\bar{x}) = 0$, and $w''(\bar{x}) \leq 0$, which implies

$$f^w(w(\bar{x}), m(\bar{x})) = -cw'(\bar{x}) - w''(\bar{x}) \geq 0,$$

that is $w(\bar{x}) \leq \phi_w(m(\bar{x}))$. The symmetric property also holds: if $w'(x) \leq 0$ for some $x > -a$, we can define $\bar{x} := \inf\{y \geq x;\, w'(y) > 0\}$, and then, $w(\bar{x}) \geq \phi_w(m(\bar{x}))$.

We repeat the argument for the function m: let $(c, w, m) \in \mathbb{R}_+ \times C^0([-a, a])^2$ be a solution of (2.7). If $m'(x) \geq 0$ for some $x > -a$, we can define $\bar{x} := \inf\{y \geq x;\, m'(y) < 0\}$, and then, $m(\bar{x}) \leq \phi_m(w(\bar{x}))$. Finally, if $m'(x) \leq 0$ for some $x > -a$, we can define $\bar{x} := \inf\{y \geq x;\, m'(y) > 0\}$, and then, $m(\bar{x}) \geq \phi_m(w(\bar{x}))$.

Step 3: phase plane analysis Notice that $(w(-a), m(-a)) = (w^*, m^*)$, and then,

$$m(-a) = \phi_m(w(-a)), \quad w(-a) = \phi_w(m(-a)). \tag{2.24}$$

We will consider now consider individually the four possible signs of $w'(-a)$, $m'(-a)$ (the cases where $w'(-a) = 0$ or $m'(-a) = 0$ will be considered further in the proof):

(i) Assume that $w'(-a) > 0$ and $m'(-a) > 0$. We define $\bar{x} := \inf\{y \geq -a;\, w'(y) < 0 \text{ or } m'(y) < 0\}$. Since w and m are increasing on $[-a, \bar{x}]$, (2.24) holds and $w \mapsto \phi_m(w)$, $m \mapsto \phi_w(m)$ are decreasing functions, we have

$$w(\bar{x}) > w(-a) = \phi_w(m(-a)) \geq \phi_w(m(\bar{x})),$$

$$m(\bar{x}) > m(-a) = \phi_m(w(-a)) \geq \phi_m(w(\bar{x})).$$

Then, $f^w(w(\bar{x}), m(\bar{x})) < 0$ and $f^m(w(\bar{x}), m(\bar{x})) < 0$. It then follows from Step 2 that $\bar{x} = a$, which means that w and m are increasing on $[-a, a]$. It is a contradiction, since $0 = w(a) < w(-a) = \bar{w}$.

Notice that the same argument would work on $[x, a]$, for any $(w(x), m(x))$ that satisfies $w(x) > \Phi_w(m(x))$, $m(x) > \Phi_m(w(x))$, $w'(x) > 0$ and $m'(x) > 0$.

(ii) Assume that $w'(-a) < 0$ and $m'(-a) < 0$. Let $\bar{x} := \inf\{y \geq -a;\, w'(y) > 0 \text{ or } m'(y) > 0\}$. Since w and m are decreasing on $[-a, \bar{x}]$, (2.24) holds and $w \mapsto \phi_m(w)$, $m \mapsto \phi_w(m)$ are decreasing functions, we have

$$w(\bar{x}) < w(-a) = \phi_w(m(-a)) \leq \phi_w(m(\bar{x})),$$

$$m(\bar{x}) < m(-a) = \phi_m(w(-a)) \leq \phi_m(w(\bar{x})).$$

It then follows from Step 2 that $\bar{x} = a$, which means that w and m are non-increasing on $[-a, a]$. Notice that this is not a contradiction, since $w(a) = 0 < w^* = w(-a)$, $m(a) = 0 < m^* = m(-a)$.

Notice that the same argument would work on $[x, a]$, for any $(w(x), m(x))$ that satisfies $\Phi_w(m(x)) > w(x)$, $m(x) < \Phi_m(w(x))$, $w'(x) < 0$ and $m'(x) < 0$.

(iii) Assume that $w'(-a) < 0$ and $m'(-a) > 0$. We define $\bar{x} := \inf\{y \geq -a;\, w'(y) > 0 \text{ or } m'(y) < 0\}$. The argument used in the two previous cases cannot be employed here. We know however that $w(\bar{x}) < w^*$, $m(\bar{x}) > m^*$. Since $m(a) = 0 < m^*$, it implies in particular that $\bar{x} < a$, and, with the notations of Lemma 2.6.7, $(w(\bar{x}), m(\bar{x})) \in \mathcal{D}_l$.

If w' changes sign in $\bar{x}$, then Step 2 implies that $w(\bar{x}) \geq \phi_w(m(\bar{x}))$, that is, with the notations of Lemma 2.6.7, $(w(\bar{x}), m(\bar{x})) \in Z_w^-$. Thanks to Lemma 2.6.7, it follows that $(w(\bar{x}), m(\bar{x})) \in Z_w^- \cap \mathcal{D}_l \subset Z_m^-$, and then $m(\bar{x}) > \phi_m(w(\bar{x}))$, which implies $-cm'(\bar{x}) - m''(\bar{x}) = f^m(w(\bar{x}), m(\bar{x})) < 0$. If $m'(\bar{x}) = 0$, then $m''(\bar{x}) > 0$, which is incompatible with the fact that $m' \geq 0$ on $[-a, \bar{x})$ and $m'(\bar{x}) = 0$. We have thus shown that $m'(\bar{x}) > 0$. Thanks to the definition of $\bar{x}$, either w is locally increasing near $\bar{x}^+$, or there exists a sequence $(x_n) \to \bar{x}^+$ such that $w'(x_{2n}) > 0$ and $w'(x_{2n+1}) < 0$. In the first case, for $\varepsilon > 0$ small enough, $w(\bar{x} + \varepsilon) > w(\bar{x}) \geq \Phi_w(m(\bar{x})) \geq \Phi_w(m(\bar{x} + \varepsilon))$ along with $w'(\bar{x} + \varepsilon) > 0$. In the second case, $w''(\bar{x}) = 0$, then $f^w(w, m)(\bar{x}) = 0$, and a simple computation shows that for $\varepsilon > 0$ small enough,

$$f^w\left(w(\bar{x} + \varepsilon), m(\bar{x} + \varepsilon)\right) = (\mu - w(\bar{x}))\varepsilon m'(\bar{x}) + o(\varepsilon) < 0,$$

where we have used the fact that $\mu - w(\bar{x}) < 0$ (since $w(\bar{x}) \geq \phi_w(m(\bar{x})) \subset \phi_w([0, K]) \subset (\mu, \infty)$, see Lemma 2.6.3). In any case, for some $\varepsilon > 0$ arbitrarily small, $w(\bar{x} + \varepsilon) > \phi_w(m(\bar{x} + \varepsilon))$, $m(\bar{x} + \varepsilon) > \phi_m(w(\bar{x} + \varepsilon))$, along with $w'(\bar{x} + \varepsilon) > 0$ and $m'(\bar{x} + \varepsilon) > 0$. argument (i) can now be applied to $(w, m)|_{[\bar{x}+\varepsilon, a]}$, leading to a contradiction.

If m' changes sign in $\bar{x}$, then Step 2 implies that $m(\bar{x}) \leq \phi_m(w(\bar{x}))$, that is, with the notations of Remark 2.6.8, $(w(\bar{x}), m(\bar{x})) \in Z_m^+$. Thanks to Remark 2.6.8, it follows that $(w(\bar{x}), m(\bar{x})) \in Z_m^+ \cap \mathcal{D}_l \subset Z_w^+$, and then $w(\bar{x}) < \phi_w(m(\bar{x}))$, which implies $-cw'(\bar{x}) - w''(\bar{x}) = f^w(w(\bar{x}), m(\bar{x})) > 0$. If $w'(\bar{x}) = 0$, then $w''(\bar{x}) < 0$, which is incompatible with the fact that $w' \leq 0$ on $[-a, \bar{x})$ and $w'(\bar{x}) = 0$. We have thus shown that $w'(\bar{x}) < 0$. Thanks to the definition of $\bar{x}$, either m is locally decreasing near $\bar{x}^+$, or there exists a sequence $(x_n) \to \bar{x}^+$ such that $m'(x_{2n}) > 0$ and $m'(x_{2n+1}) < 0$. In the first case, for $\varepsilon > 0$ small enough, $m(\bar{x}+\varepsilon) < m(\bar{x}) \leq \Phi_m(w(\bar{x})) \leq \Phi_m(w(\bar{x}+\varepsilon))$ along with $m'(\bar{x}+\varepsilon) > 0$. In the second case, $m''(\bar{x}) = 0$, then $f^m(w,m)(\bar{x}) = 0$, and a simple computation shows that for $\varepsilon > 0$ small enough,

$$f^m\left(w(\bar{x}+\varepsilon), m(\bar{x}+\varepsilon)\right) = \left(\mu - \frac{r}{K}m(\bar{x})\right)\varepsilon w'(\bar{x})) + o(\varepsilon) > 0,$$

where we have used the fact that $\mu - \frac{r}{K}m(\bar{x}) < 0$ (since $m(\bar{x}) > m^* = \phi_m(w^*) \subset \phi_m([0,1]) \subset (\mu K/r, \infty)$, see Lemma 2.6.3). In both cases, argument (ii) can now be applied to $(w,m)|_{[\bar{x}+\varepsilon,a]}$, which is not a contradiction, since $w(a) = 0 < w(\bar{x})$, $m(a) = 0 < m(\bar{x})$.

(iv) Assume that $w'(-a) > 0$ and $m'(-a) < 0$. We define $\bar{x} := \inf\{y \geq -a;\, w'(y) < 0 \text{ or } m'(y) > 0\}$. Then $w(\bar{x}) > w^*$, $m(\bar{x}) < m^*$. Since $m(a) = 0 < m^*$, it implies in particular that $\bar{x} < a$, and, with the notations of Lemma 2.6.7, $(w(\bar{x}), m(\bar{x})) \in \mathcal{D}_r$.

If w' changes sign in $\bar{x}$, then Step 2 implies that $w(\bar{x}) \leq \phi_w(m(\bar{x}))$, that is, with the notations of Remark 2.6.8, $(w(\bar{x}), m(\bar{x})) \in Z_w^+$. Thanks to Remark 2.6.8, it follows that $(w(\bar{x}), m(\bar{x})) \in Z_w^+ \cap \mathcal{D}_r \subset Z_m^+$, and then $m(\bar{x}) < \phi_m(w(\bar{x}))$, which implies $-cm'(\bar{x}) - m''(\bar{x}) = f^m(w(\bar{x}), m(\bar{x})) > 0$. If $m'(\bar{x}) = 0$, then $m''(\bar{x}) < 0$, which is incompatible with the fact that $m' \leq 0$ on $[-a, \bar{x})$ and $m'(\bar{x}) = 0$. We have thus shown that $m'(\bar{x}) < 0$. Thanks to the definition of $\bar{x}$, either w is locally decreasing near $\bar{x}^+$, or there exists a sequence $(x_n) \to \bar{x}^+$ such that $w'(x_{2n}) > 0$ and $w'(x_{2n+1}) < 0$. In the first case, for $\varepsilon > 0$ small enough, $w(\bar{x}+\varepsilon) < w(\bar{x}) \leq \Phi_w(m(\bar{x})) \leq \Phi_w(m(\bar{x}+\varepsilon))$ along with $w'(\bar{x}+\varepsilon) < 0$. In the second case, $w''(\bar{x}) = 0$, then $f^w(w,m)(\bar{x}) = 0$, and a simple computation shows that for $\varepsilon > 0$ small enough,

$$f^w(w,m)(\bar{x}+\varepsilon) = (\mu - w(\bar{x}))\varepsilon m'(\bar{x}) + o(\varepsilon) > 0,$$

where we have used the fact that $\mu - w(\bar{x}) < 0$ (since $w(\bar{x}) > w^* = \phi_w(m^*) \subset \phi_w([0,1]) \subset (\mu, \infty)$, see Lemma 2.6.3). In both cases, argument (ii) can now be applied to $(w,m)|_{[\bar{x}+\varepsilon,a]}$, which is not a contradiction, since $w(a) = 0 < w(\bar{x})$, $m(a) = 0 < m(\bar{x})$.

If m' changes sign in $\bar{x}$, then Step 2 implies that $m(\bar{x}) \geq \phi_m(w(\bar{x}))$, that is, with the notations of Lemma 2.6.7, $(w(\bar{x}), m(\bar{x})) \in Z_m^-$. Thanks to Lemma 2.6.7, it follows that $(w(\bar{x}), m(\bar{x})) \in Z_m^- \cap \mathcal{D}_r \subset Z_w^-$, and then $w(\bar{x}) > \phi_w(m(\bar{x}))$, which implies $-cw'(\bar{x}) - w''(\bar{x}) = f^w(w(\bar{x}), m(\bar{x})) < 0$. If $w'(\bar{x}) = 0$, then $w''(\bar{x}) > 0$, which is incompatible with the fact that $w' \geq 0$ on $[-a, \bar{x})$ and $w'(\bar{x}) = 0$. We have thus shown that $w'(\bar{x}) > 0$. Thanks to the definition of $\bar{x}$, either m is locally increasing near $\bar{x}^+$, or there exists a sequence $(x_n) \to \bar{x}^+$ such that $m'(x_{2n}) > 0$ and $m'(x_{2n+1}) < 0$. In the first case, for $\varepsilon > 0$ small enough, $m(\bar{x}+\varepsilon) > m(\bar{x}) \geq \Phi_m(w(\bar{x})) \geq \Phi_m(w(\bar{x}+\varepsilon))$ along with $m'(\bar{x}+\varepsilon) > 0$. In the second case, $m''(\bar{x}) = 0$, then $f^m(w,m)(\bar{x}) =$

0, and a simple computation shows that for $\varepsilon > 0$ small enough,

$$f^m(w,m)(\bar{x}+\varepsilon) = \Big(\mu - \frac{r}{K}m(\bar{x})\Big)\, \varepsilon w'(\bar{x}) + o(\varepsilon) < 0,$$

where we have used the fact that $\mu - \frac{r}{K}m(\bar{x}) < 0$ (since $m(\bar{x}) \geq \phi_m(w(\bar{x})) \subset \phi_m([0,1]) \subset (\mu K/r, \infty)$, see Lemma 2.6.3). In both cases, argument (i) can now be applied to $(w,m)|_{[\bar{x}+\varepsilon,a]}$, leading to a contradiction.

Let consider now the case where $w'(-a) = 0$ or $m'(-a) = 0$. If $w'(-a) = m'(-a) = 0$, then $w \equiv w^*$, $m \equiv m^*$, which is a contradiction. Assume w.l.o.g. that $w'(-a) \neq 0$. If there exists $\varepsilon > 0$ such that for any $x \in [-a, -a+\varepsilon]$, $m'(x) = 0$, then m is constant on the interval $[-a, -a+\varepsilon]$, and then $f^m(w(x), m(x)) = 0$ for $x \in [-a, -a+\varepsilon]$. This implies in turn that $m(x) = \phi_m(w(x))$, and then w is constant on $[-a, -a+\varepsilon]$, since ϕ_m is a decreasing function, which is a contradiction. There exists thus a sequence $x_n \to -a$, $x_n > -a$, such that $w(x_n) \neq w^*$, and $\mathrm{sgn}(m(x_n) - m^*) = \mathrm{sgn}(m'(x_n)) \neq 0$, while $\mathrm{sgn}(w(x_n) - w^*) = \mathrm{sgn}(w'(0)) \neq 0$. The above argument (i-iv) can therefore be reproduced for $(w,m)|_{[x_n,a]}$.

Finally, the fact that $\bar{x} \leq 0$ is a consequence of the inequality $w(0) + m(0) < \min(w^*, m^*)$. □

Proposition 2.4.2. *Let r, K, μ satisfy Assumption 2.1.1. Let $(c,w,m) \in \mathbb{R}_+ \times C^0(\mathbb{R})^2$ be a solution of (2.3) constructed in Theorem 2.2.1. Then, there exists $\bar{x} \in [-\infty, 0)$ such that*

- *either w is decreasing on $\mathbb{R}$, while m is increasing on $(-\infty, \bar{x}]$ and decreasing on $[\bar{x}, \infty)$,*
- *or m is decreasing on $\mathbb{R}$, while w is increasing on $(-\infty, \bar{x}]$ and decreasing on $[\bar{x}, \infty)$,*

Moreover,

$$w(x) \to w^*, \quad m(x) \to m^* \text{ as } x \to -\infty.$$

Proof of Proposition 2.4.2. The travelling wave (c,w,m) constructed in Theorem 2.2.1 is obtained as a limit (in $L^\infty_{loc}(\mathbb{R})$) of solutions $(w_n, m_n, c_n) \in \mathbb{R}_+ \times C^0([-a_n, a_n])^2$ of (2.7) on $[-a_n, a_n]$, with $a_n \underset{n\to\infty}{\longrightarrow} \infty$. Each of those solutions then satisfy one of the two the monotonicity properties of Lemma 2.4.1. In particular, there is at least one of those properties that is satisfied by an infinite sequence of solutions (w_n, m_n, c_n). We may then assume w.l.o.g. that all the solutions (w_n, m_n, c_n) satisfy the first monotonicity property in Lemma 2.4.1. We assume therefore that for all $n \in \mathbb{N}$, there exists $\bar{x}_n \in [-a_n, 0)$ such that w_n is decreasing on $[-a_n, a_n]$, while m_n is increasing on $[-a_n, \bar{x}_n]$ and decreasing on $[\bar{x}_n, a_n]$. Up to an extraction, we can define $\bar{x} := \lim_{n\to\infty} a_n \in [-\infty, 0]$. Then, w is a uniform limit of decreasing function on any bounded interval, and is thus decreasing. Let now $\tilde{x} > \bar{x}$.

m_n is then a decreasing function on $[\tilde{x}, \infty) \cap [-a_n, a_n]$ for n large enough, and $m|_{[\tilde{x},\infty)}$ is thus a uniform limit of decreasing functions on any bouded interval of $[\tilde{x}, \infty)$. This implies that m is decreasing on $[\bar{x}, \infty)$. A similar argument shows that m is increasing on $(-\infty, \bar{x}]$, if $\bar{x} > -\infty$. the case where all the solutions (w_n, m_n, c_n) satisfy the second monotonicity property in Lemma 2.4.1 can be treated similarly.

We have shown in particular that w, m are monotonic on $(-\infty, \tilde{x})$, for some $\tilde{x} < 0$ ($\tilde{x} = \bar{x}$ if $\bar{x} > -\infty$, $\tilde{x} = 0$ otherwise). Since w and m are regular bounded functions, it implies that

$$f^w(w(x), m(x)) = -cw'(x) - w''(x) \to 0,$$

$$f^m(w(x), m(x)) = -cm'(x) - m''(x) \to 0,$$

as $x \to -\infty$. This combined to $\liminf_{x\to-\infty} w(x) + m(x) > 0$ and $(w, m) \in [0, 1] \times [0, K]$ implies that $w(x) \to w^*$ and $m(x) \to m^*$ as $x \to -\infty$. $\square$

2.4.2 Case of a small mutation rate

The result of this subsection shows that if $\mu > 0$ is small, then only the first situation described in Lemma 2.4.1, with $\bar{x} > -\infty$, is possible.

Proposition 2.4.3. *Let r, K, μ satisfy Assumption 2.1.1. Let $(c, w, m) \in \mathbb{R}_+ \times C^0(\mathbb{R})$ be a solution of (2.3) constructed in Theorem 2.2.1. There exists $\bar{\mu} = \bar{\mu}(r, K) > 0$ such that $\mu < \bar{\mu}$ implies that w is decreasing on $\mathbb{R}$, while m is increasing on $(-\infty, \bar{x}]$ and decreasing on $[\bar{x}, \infty)$, for some $\bar{x} \in \mathbb{R}_-$.*

Proof of Proposition 2.4.3. Notice that the solution (c, w, m) satisfies the assumptions of Proposition 2.4.2.

Let us assume that $\|m\|_\infty \le m^*$. We will show that this assumption leads to a contradiction if $\mu > 0$ is small. Let $\bar{x} = \max\{x > -\infty;\, w(x) \ge m^*\}$. Then w satisfies $-cw' - w'' \le (1 - \mu)w + \mu m^*$ on $(-\infty, \bar{x}]$. Since (c, w, m) satisfies the assumptions of Proposition 2.4.2 and $w(\bar{x}) = m^* < w^*$, we have that $w(x) \ge m^*$ for all $x \le \bar{x}$. w thus satisfies $-cw' - w'' \le w$ on $(-\infty, \bar{x}]$. We define now

$$\bar{w}(x) = m^* \, e^{\frac{c-\sqrt{c^2-4}}{2}(\bar{x}-x)},$$

which satisfies $-c\bar{w}' - \bar{w}'' = \bar{w}$ on $(-\infty, \bar{x}]$, $\bar{w}(\bar{x}) = w(\bar{x})$, and $\bar{w}(y) \ge 1 \ge w(y)$ for $y << 0$. Since w is bounded, $\alpha\bar{w} > w$ for $\alpha > 0$ large enough. We can then define $\alpha^* := \min\{\alpha > 0;\, \alpha\bar{w} > w \text{ on } (-\infty, \bar{x})\}$. If $\alpha^* > 1$, there exists $x^* \in (-\infty, \bar{x})$ such that $\alpha^*\bar{w}(x^*) = w(x^*)$, and then, $-c(\alpha^*\bar{w} - w)'(x^*) - (\alpha^*\bar{w} - w)''(x^*) > \alpha^*\bar{w}(x^*) - w(x^*) = 0$, which is a contradiction, since $\alpha^*\bar{w} > w$ implies that $-c(\alpha^*\bar{w} - w)'(x^*) - (\alpha^*\bar{w} - w)''(x^*) \le 0$. Thus,

$$w(x) \le \bar{w}(x), \text{ for } x \in (-\infty, \bar{x}]. \tag{2.25}$$

In particular, if we define

$$\tilde{x} := \bar{x} - \frac{2}{c - \sqrt{c^2 - 4}} \ln\left(\frac{K}{m^*}\left(\frac{1}{2} - \frac{\mu}{r} - \frac{1}{2r}\right) - 1\right), \tag{2.26}$$

then $w(x) \leq K\left(\frac{1}{2} - \frac{\mu}{r} - \frac{1}{2r}\right) - m^*$ on $[\tilde{x}, \bar{x}]$. Notice that $m^* \to 0$ as $\mu \to 0$ (see Lemma 2.6.9), and then $\frac{K}{m^*}\left(\frac{1}{2} - \frac{\mu}{r} - \frac{1}{2r}\right) \to \infty$ as $\mu \to 0$; $\tilde{x}$ is then well defined as soon as $\mu > 0$ is small enough, and $\tilde{x} - \bar{x} \to -\infty$ as $\mu \to 0$. This estimate applied to the equation on m (see (2.3)), implies, for $x \in [\tilde{x}, \bar{x}]$, that

$$-cm'(x) - m''(x) \geq r\left(1 - \frac{\mu}{r} - \frac{m^* + w(x)}{K}\right) m(x) + \mu\, w \geq \frac{1+r}{2} m + \mu\, m^*,$$

where we have also used the fact that $w \geq m^*$ on $(-\infty, \bar{x}]$.

We define next

$$\bar{m}_1 := -\frac{\mu\, m^*}{c+2}(x - \bar{x})\,(x - (\bar{x} - 1))\,,$$

which satisfies $-c\bar{m}_1' - \bar{m}_1'' \leq \mu m^*$ as well as $\bar{m}_1\,(\bar{x} - 1) = 0 \leq m\,(\bar{x} - 1)$ and $\bar{m}_1(\bar{x}) = 0 \leq m(\bar{x})$. The weak maximum principle [108, Theorem 8.1] then implies that $m(x) \geq \bar{m}_1(x)$ for all $x \in [\bar{x} - 1, \bar{x}]$, and in particular,

$$m(\bar{x} - 1/2) \geq \frac{\mu\, m^*}{4(c+2)}.$$

We define (we recall the definition (2.26) of $\tilde{x}$)

$$\bar{m}_2 := \frac{\mu\, m^*}{4(c+2)} e^{\frac{c - \sqrt{c^2 - 2(1+r)}}{2}(\bar{x} - 1/2 - x)} - A e^{\frac{c}{2}(\bar{x} - 1/2 - x)},$$

with $A = \frac{\mu\, m^*}{4(c+2)} e^{-\frac{\sqrt{c^2 - 2(r+1)}}{2}(\bar{x} - 1/2 - \tilde{x})}$, so that $\bar{m}_2(\tilde{x}) = 0$. $\bar{m}_2$ then satisfies $-c\bar{m}_2' - \bar{m}_2'' < \frac{(1+r)}{2}\bar{m}_2$, since $c(c/2) - (c/2)^2 > \frac{1+r}{2}$ (see (2.5)). Let now

$$\alpha^* := \max\{\alpha; m(x) \geq \alpha \bar{m}_2(x),\ \forall x \in [\tilde{x}, \bar{x} - 1/2]\}.$$

$\alpha^* > 0$, since $\min_{[\tilde{x}, \bar{x} - 1/2]} m > 0$. If $\alpha^* < 1$, then $\alpha^* \bar{m}_2(\bar{x} - 1/2) < \frac{\mu\, m^*}{4(c+2)} \leq m(\bar{x} - 1/2)$, while $\alpha^* \bar{m}_2(\tilde{x}) = 0 < m(\tilde{x})$. Then $\alpha^* \bar{m}_2 \leq m$ on $[\tilde{x}, \bar{x} - 1/2]$, and there exists $x^* \in [\tilde{x}, \bar{x} - 1/2]$ such that $\alpha^* \bar{m}_2(x^*) = m(x^*)$, and

$$0 \leq -c(\bar{m}_2 - m)'(x^*) - (\bar{m}_2 - m)''(x^*) < \frac{(1+r)}{2}(\bar{m}_2 - m)(x^*) = 0,$$

which is a contradiction. We have thus proven that $m \geq \bar{m}_2$ on $[\tilde{x}, \bar{x} - 1/2]$, and in particular, for $\mu > 0$ small enough,

$$\begin{aligned} \|m\|_\infty \geq \bar{m}_2\left(\tilde{x} + \frac{2\ln(2)}{\sqrt{c^2 - 2(1+r)}}\right) \\ = \frac{\mu\, m^*}{4(c+2)} e^{\frac{c \ln 2}{\sqrt{c^2 - 2(1+r)}}} e^{\frac{c - \sqrt{c^2 - 2(1+r)}}{2}(\bar{x} - 1/2 - \tilde{x})}. \end{aligned}$$

We recall indeed that $\tilde{x} - \bar{x} \to -\infty$ as $\mu \to 0$, and then $\tilde{x} + \frac{2\ln(2)}{\sqrt{c^2-2(1+r)}} \in [\tilde{x}, \bar{x} - 1/2]$ if $\mu > 0$ is small enough. Thanks to the definition of $\tilde{x}$, this inequality can be written

$$\begin{aligned}\ln\left(\frac{4(c+2)\|m\|_\infty}{\mu\, m^*}\right) - \frac{c\ln 2}{\sqrt{c^2-2(1+r)}} \\ \geq \frac{c-\sqrt{c^2-2(1+r)}}{2}\Bigg(-\frac{1}{2} + \frac{2}{c-\sqrt{c^2-4}} \\ \times \ln\left(\frac{K}{m^*}\left(\frac{1}{2}-\frac{\mu}{r}-\frac{1}{2r}\right)-1\right)\Bigg).\end{aligned}$$

We have assumed that $\|m\|_\infty = m^*$, thus, if we denote by $\mathcal{O}_{\mu\sim 0^+}(1)$ a function of $\mu > 0$ that is bounded for μ small enough, we get

$$\ln\left(\frac{1}{\mu}\right) + \mathcal{O}_{\mu\sim 0^+}(1) \geq \frac{c-\sqrt{c^2-2(1+r)}}{c-\sqrt{c^2-4}}\ln\left(\frac{1}{m^*}\right).$$

Moreover, we know that $m^* \leq C\mu$ for some $C > 0$, see Lemma 2.6.9. Then,

$$\ln\left(\frac{1}{\mu}\right) + \mathcal{O}_{\mu\sim 0^+}(1) \geq \frac{c-\sqrt{c^2-2(1+r)}}{c-\sqrt{c^2-4}}\ln\left(\frac{1}{\mu}\right),$$

which is a contradiction as soon as $\mu > 0$ is small, since $r > 1$.

We have thus proved that for $\mu > 0$ small enough, we have $\|m\|_\infty > m^*$. This estimate combined to Proposition 2.4.2 proves Proposition 2.4.3. □

2.5 Proof of Theorem 2.2.3

Notice first that if we chose $\varepsilon > 0$ small enough, then $0 < \mu < K < \varepsilon$ implies that Assumption 2.1.1 is satisfied.

We will need the following estimate on the behavior of travelling waves of (2.3):

Proposition 2.5.1. *Let r, K, μ satisfy Assumption 2.1.1. Let $(c, w, m) \in \mathbb{R}_+ \times C^\infty(\mathbb{R}) \times C^\infty(\mathbb{R})$ be a solution of (2.3), such that $\liminf_{x\to-\infty}(w(x)+m(x)) > 0$. Then, $\liminf_{x\to-\infty} w(x) \geq 1-\mu-K$.*

Moreover, if $w(\bar{x}) < 1-K-\mu$ for some $\bar{x} \in \mathbb{R}$, then w is decreasing on $[\bar{x}, \infty)$.

Proof of Proposition 2.5.1. Since $m(x) < K$ for all $x \in \mathbb{R}$, any local minimum $\bar{x}$ of w satisfies

$$\begin{aligned}0 &\geq -cw'(\bar{x}) - w''(\bar{x}) = (1-\mu-w(\bar{x})-m(\bar{x}))w(\bar{x}) + \mu m(\bar{x}) \\ &> (1-\mu-K-w(\bar{x}))w(\bar{x}),\end{aligned} \tag{2.27}$$

and then $w(\bar{x}) \geq 1-\mu-K$.

Assume that $\liminf_{x\to -\infty} w(x) < 1-\mu-K$. Then, $x \mapsto w(x)$ can not have a minimum for $x << 0$, and is thus monotone for $x << 0$. Then $l := \lim_{x\to-\infty} w(x) \in [0, 1-\mu-K]$ exists and $w'(x) \to_{x\to-\infty} 0$, $w''(x) \to_{x\to-\infty} 0$. This implies $-cw'(x) - w''(x) \to_{x\to\infty} 0$, which, coupled to (2.27) implies that $l=0$ or $l = 1-\mu-K$. $l=0$ leads to a contradiction, since $\liminf_{x\to-\infty}(w(x)+m(x)) > 0$, which proves the first assertion.

To prove the second assertion, we notice that since w cannot have a minimum $\tilde{x} \in \mathbb{R}$ such that $w(\tilde{x}) < 1-K-\mu$, w is monotonic on $\{x \in \mathbb{R};\ w(x) < 1-K-\mu\}$. This monotony combined to $\liminf_{x\to-\infty} w(x) \geq 1-\mu-K > w(\bar{x})$ implies that w is decreasing on $[\bar{x}, \infty)$. $\square$

The main idea of the proof of theorem 2.2.3 is to compare w to solutions of modified Fisher-KPP equations, which we introduce in the following Lemma:

Lemma 2.5.2. *Let r, K, μ satisfy Assumptions 2.1.1. Let $(c, w, m) \in \mathbb{R}_+ \times C^\infty(\mathbb{R}) \times C^\infty(\mathbb{R})$ be a solution of (2.3), with $c \geq 2+K$. Let also $\overline{w} \in C^\infty(\mathbb{R})$, $\underline{w} \in C^\infty(\mathbb{R})$ solutions of*

$$\begin{cases} -c\overline{w}' - \overline{w}'' = \overline{w}(1-\overline{w}) + K, \\ \overline{w}(x) \to_{x\to-\infty} \frac{1+\sqrt{1+4K}}{2},\ \overline{w}(x) \to_{x\to+\infty} -\frac{\sqrt{1+4K}-1}{2}, \end{cases} \tag{2.28}$$

$$\begin{cases} -c\underline{w}' - \underline{w}'' = \underline{w}(1-2K-\underline{w}), \\ \underline{w}(x) \to_{x\to-\infty} 1-2K,\ \underline{w}(x) \to_{x\to+\infty} 0. \end{cases} \tag{2.29}$$

Assume $\underline{w}(0) \leqslant w(0) \leqslant \overline{w}(0)$. Then

$$\forall x \leqslant 0, \qquad \underline{w}(x) \leqslant w(x) \leqslant \overline{w}(x).$$

Remark 2.5.3. Notice that $\overline{w} + \frac{\sqrt{1+4K}-1}{2}$ and $\underline{w}$ are solution of a classical Fisher-KPP equation $-cu' - u'' = u(a-bu)$ with $a \in (0, 1+2K)$, $b > 0$, and a speed $c \geq 2\sqrt{a}$. The existence, uniqueness (up to a translation) and monotony of $\overline{w}$ and $\underline{w}$ are thus classical results (see e.g. [141]). Thanks to those relations, the argument developed in this section can indeed be seen as a precise analysis on the profile of $x \mapsto u(x)$ for $x > 0$ large.

Proof of Lemma 2.5.2. To prove this lemma, we use a sliding method.

- Let $\underline{w}_\eta(x) := \underline{w}(x+\eta)$. Thanks to Proposition 2.5.1, there exists $x_0 \in \mathbb{R}$ such that $w(x) > 1-2K = \sup_{\mathbb{R}} \underline{w}_\eta$ for all $x \leq x_0$ (we recall that $\mu < K$). Since $\lim_{x\to\infty} \underline{w}(x) = 0$, there exists $x^0 > 0$ such that $\underline{w}(x) < \min_{[x_0,0]} w$ for all $x > x^0$. Then, for $\eta \geq x_0 + x^0$,

$$\underline{w}_\eta(x) < w(x), \quad \forall x \leqslant 0.$$

We can then define $\overline{\eta} := \inf\{\eta, \forall x \leqslant 0, \underline{w}_\eta(x) \leqslant w(x)\}$. We have then $\underline{w}_{\overline{\eta}}(x) \leqslant w(x)$ for all $x \leq 0$. If $\overline{\eta} > 0$, since $\inf_{(-\infty,x_0]} w > 1 - 2K = \sup_{\mathbb{R}} \underline{w}_\eta$ and $\underline{w}_{\overline{\eta}}(0) = \overline{w}(\eta) < \overline{w}(0) \leq w(0)$ (we recall that $\underline{w}$ is decreasing, see Remark 2.5.3), there exists $\underline{x} \in (x_0, 0)$ such that $\underline{w}_{\overline{\eta}}(\underline{x}) = w(\underline{x})$. $\underline{x}$ is then a minimum of $w - \underline{w}_{\overline{\eta}}$, and thus

$$\begin{aligned}
0 &\geq -c(w - \underline{w}_{\overline{\eta}})'(\underline{x}) - (w - \underline{w}_{\overline{\eta}})''(\underline{x}) \\
&= w(\underline{x})(1 - \mu - m(\underline{x}) - w(\underline{x})) + \mu m(\underline{x}) - \underline{w}_{\overline{\eta}}(\underline{x})(1 - 2K - \underline{w}_{\overline{\eta}}(\underline{x})) \\
&> w(\underline{x})(1 - 2K - w(\underline{x})) - \underline{w}_{\overline{\eta}}(\underline{x})(1 - 2K - \underline{w}_{\overline{\eta}}(\underline{x})) = 0, \qquad (2.30)
\end{aligned}$$

where we have used the estimate $\|m\|_\infty \leq K$ obtained in Proposition 2.3.3. (2.30) is a contradiction, we have then shown that $\bar{\eta} \leq 0$, and thus, for all $x \leq 0$, $\underline{w}(x) \leq w(x)$.

- Similarly, let $\overline{w}_\eta(x) := \overline{w}(x - \eta)$. Since $\lim_{x\to-\infty} \overline{w}(x) > 1$ and w satisfies the estimate of Proposition 2.3.3, we have, for $\eta \in \mathbb{R}$ large enough,

$$\forall x \leqslant 0, \quad w(x) < 1 < \overline{w}_\eta(x).$$

We can then define $\overline{\eta} := \inf\{\eta, \forall x \leqslant 0, w(x) \leqslant \overline{w}_\eta(x)\}$. We have then $w(x) \leqslant \overline{w}_{\overline{\eta}}$ for all $x \leq 0$. If $\overline{\eta} > 0$, since $\sup_{\mathbb{R}} w < 1 < \lim_{x\to-\infty} \overline{w}(x)$ and $w(0) \leq \overline{w}(0) < \overline{w}(-\overline{\eta}) = \overline{w}_{\bar{\eta}}(0)$ (we recall that $\overline{w}$ is decreasing, see Remark 2.5.3), there exists $\bar{x} < 0$ such that $w(\underline{x}) = \overline{w}_{\overline{\eta}}(\underline{x})$. $\bar{x}$ is then a minimum of $\overline{w}_{\overline{\eta}} - w$, and thus

$$\begin{aligned}
0 &\geq -c(\overline{w}_{\overline{\eta}} - w)'(\bar{x}) - (\overline{w}_{\overline{\eta}} - w)''(\bar{x}) \\
&= \overline{w}_{\overline{\eta}}(\bar{x})(1 - \overline{w}_{\overline{\eta}}(\bar{x})) + K - w(\bar{x})(1 - \mu - w(\bar{x}) - m(\bar{x})) - \mu m(\bar{x}) \\
&> \overline{w}_{\overline{\eta}}(\bar{x})(1 - \overline{w}_{\overline{\eta}}(\bar{x})) - w(\bar{x})(1 - w(\bar{x})) = 0,
\end{aligned}$$

which is a contradiction. We have then shown that $\bar{\eta} \leq 0$, and thus, for all $x \leq 0$, $w(x) \leq \overline{w}(x)$. □

We also need to compare the solution of the Fisher-KPP equation with speed c to the solutions of the modified Fisher-KPP equations introduced in Lemma 2.5.2.

Lemma 2.5.4. *Let r, K, μ satisfy Assumption 2.1.1, and $c \geq 2 + K$. Let (c, u), with $u \in C^\infty(\mathbb{R})$, be a travelling wave of the Fisher-KPP equation, see* (2.6). *Let also $\overline{w}$, $\underline{w}$ solutions of* (2.28) *and* (2.29) *respectively. Assume $\underline{w}(0) \leqslant u(0) \leqslant \overline{w}(0)$. Then*

$$\forall x \leqslant 0, \qquad \underline{w}(x) \leqslant u(x) \leqslant \overline{w}(x).$$

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The arguments of the proof of Lemma 2.5.2 can be used to prove Lemma 2.5.4. We omit the details.

We can now prove theorem 2.2.3.

Proof of Theorem 2.2.3. Notice first that $c_* > 2+K$, provided K, $\mu > 0$ are small enough. Let $\overline{w} \in C^\infty(\mathbb{R})$ and $\underline{w} \in C^\infty(\mathbb{R})$ satisfying (2.28) and (2.29) respectively. $\overline{w}$ and $\underline{w}$ are then decreasing (see Remark 2.5.3), and we may assume (up to a translation) that they satisfy $\underline{w}(0) = w(0) = u(0) = \overline{w}(0)$. Then Lemma 2.5.2 and 2.5.4 imply that $\underline{w}(x) \leqslant w(x), u(x) \leqslant \overline{w}(x)$ for $x \leq 0$, and then, $\|w - u\|_{L^\infty(-\infty,0]} \leqslant \|\overline{w} - \underline{w}\|_{L^\infty(-\infty,0]}$.

Let $\tilde{w} = \overline{w} - \underline{w} \geqslant 0$, which satisfies

$$-c\tilde{w}' - \tilde{w}'' = \tilde{w}(1 - (\overline{w} + \underline{w})) + K + 2K\underline{w}.$$

We estimate first the maximum of $\tilde{w}$ over $\{x \in \mathbb{R};\ \underline{w}(x) \leqslant 3/4 - K\}$ to prove the estimate on $\|\tilde{w}\|_{L^\infty(-\infty,0]}$ stated in Theorem 2.2.3. If $\underline{w} \leqslant 3/4-K$, then

$$-c\underline{w}' - \underline{w}'' \geqslant \underline{w}(1/4 - K). \tag{2.31}$$

Let

$$\lambda_+ := \frac{c + \sqrt{c^2 - 4(1/4 - K)}}{2}, \qquad \lambda_- := \frac{c - \sqrt{c^2 - 4(1/4 - K)}}{2},$$

and $\varphi(x) := e^{-\lambda_- x} - e^{-\lambda_+ x}$. Then φ satisfies $-c\varphi' - \varphi'' = (1/4 - K)\varphi$, $\varphi(-\infty) = -\infty$ and $\varphi(+\infty) = 0$. Moreover, φ is positive when $x > 0$ and negative when $x < 0$. Finally, the maximum of φ is attained at $\overline{x} := \frac{\ln\lambda_+ - \ln\lambda_-}{\lambda_+ - \lambda_-} > 0$. One can show that $\varphi(\bar{x})$ is a continuous and positive function of c and K, which is uniformly bounded away from 0 for $K \in (0, 1/8)$ and $c \in [2, \infty)$. There exists thus a universal constant $C > 0$ such that $\varphi(\bar{x}) > C > 0$, for any $K \in (0, 1/8)$, $c \in [2, \infty)$. Let $\gamma \in (0, 3/4 - K)$ and φ^γ defined by

$$\varphi^\gamma(x) := \gamma\frac{\varphi(x)}{\varphi(\bar{x})},$$

and $\varphi^\gamma_\eta(x) := \varphi^\gamma(x + \eta)$ for $\eta \in \mathbb{R}$. Since (for $K > 0$ small) $\max_{\mathbb{R}} \varphi^\gamma \leq 3/4 - K < 1 - 2K = \lim_{x\to-\infty} \underline{w}(x)$ and $\lim_{\eta\to\infty} \varphi^\gamma_\eta(0) = \lim_{x\to\infty} \varphi^\gamma(x) = 0 < \underline{w}(0)$, we have that for $\eta > 0$ large enough,

$$\forall x \leqslant 0, \quad \varphi^\gamma_\eta(x) \leqslant \underline{w}(x).$$

Let $\tilde{\eta} := \inf\{\eta \in \mathbb{R};\ \forall x \leqslant 0,\ \varphi^\gamma_\eta(x) \leqslant \underline{w}(x)\}$. Then $\varphi^\gamma_{\tilde{\eta}} \leq \underline{w}$ on $(-\infty, 0]$, and since $\varphi^\gamma_{\tilde{\eta}}(x) < 0$ for $x << 0$, either $\underline{w}(0) = \varphi^\gamma_{\tilde{\eta}}(0)$, or there exists $\tilde{x} \in (-\infty, 0)$

such that $\underline{w}(\tilde{x}) = \varphi_{\tilde{\eta}}^{\gamma}(\tilde{x})$. In the latter case, $\tilde{x}$ is the minimum of $\underline{w} - \varphi_{\tilde{\eta}}^{\gamma}$, and then

$$\begin{aligned} 0 &\geq -c(\underline{w} - \varphi_{\tilde{\eta}}^{\gamma})'(\tilde{x}) - (\underline{w} - \varphi_{\tilde{\eta}}^{\gamma})''(\tilde{x}) \\ &= (1 - 2K - \underline{w}(\tilde{x}))\underline{w}(\tilde{x}) - (1/4 - K)\varphi_{\tilde{\eta}}^{\gamma}(\tilde{x}) \\ &\geq (3/4 - K - \underline{w}(\tilde{x}))\,\underline{w}(\tilde{x}) > 0, \end{aligned}$$

since $\underline{w}(\tilde{x}) = \varphi_{\tilde{\eta}}^{\gamma}(\tilde{x}) \leq \gamma < 3/4 - K$. The above estimate is a contradiction, which implies $\underline{w}(0) = \varphi_{\tilde{\eta}}^{\gamma}(0)$. Then

$$(e^{-\lambda_- \tilde{\eta}} - e^{-\lambda_+ \tilde{\eta}}) = \frac{w(0)}{\gamma} \left(e^{-\lambda_- \overline{x}} - e^{-\lambda_+ \overline{x}} \right),$$

and then

$$-\lambda_- \tilde{\eta} \geq \ln \left(\frac{w(0)}{\gamma} \left(e^{-\lambda_- \overline{x}} - e^{-\lambda_+ \overline{x}} \right) \right),$$

which implies $\varphi_{\eta}^{\gamma}(x) \leq \underline{w}(x)$ for all $x \in (-\infty, 0]$, with $\gamma \in (0, 3/4 - K)$ and $\eta = -\frac{1}{\lambda_-} \ln \left(\frac{w(0)}{\gamma} (e^{-\lambda_- \overline{x}} - e^{-\lambda_+ \overline{x}}) \right)$. Passing to the limit $\gamma \to 3/4 - K$, we then get that $\varphi_{\overline{\eta}}^{3/4-K}(x) \leq \underline{w}(x)$ for all $x \in (-\infty, 0]$, with

$$\overline{\eta} := -\frac{1}{\lambda_-} \ln \left(\frac{w(0)}{3/4 - K} \left(e^{-\lambda_- \overline{x}} - e^{-\lambda_+ \overline{x}} \right) \right).$$

In particular, $\varphi_{\overline{\eta}}^{3/4-K} \leq \underline{w}$ implies that $\{x \in (-\infty, 0];\ \underline{w}(x) \leqslant 3/4 - K\} \subset [\min(0, \overline{x} - \overline{\eta}), 0] \subset [\min(0, -\overline{\eta}), 0]$ (indeed, $-\overline{\eta} < 0$ if $w(0)$ is small enough).

Since $\sup_{\mathbb{R}} \underline{w} = 1 - 2K$, we have

$$-c\tilde{w}' - \tilde{w}'' = \tilde{w}(1 - (\underline{w} + \overline{w})) + K + 2K\underline{w} < \tilde{w} + K(3 - 4K),$$

and $\tilde{w}(0) = 0$. We can then introduce $\psi(x) = K(3 - 4K)\,(e^{-\alpha x} - 1)$, with $\alpha = \frac{c - \sqrt{c^2 - 4}}{2}$ which satisfies $-c\psi' - \psi'' = \psi + K(3 - 4K)$. A sliding argument (that we skip here) shows that

$$\forall x \leq 0, \quad \tilde{w}(x) \leqslant \psi(x) = K(3 - 4K) \left(e^{-\alpha x} - 1 \right).$$

This estimate implies that

$$\begin{aligned} \max_{[-\overline{\eta}, 0]} \tilde{w} \leqslant K(3 - 4K) \exp \left(-\frac{\alpha}{\lambda_-} \ln \left(\frac{w(0)}{3/4 - K} \left(e^{-\lambda_- \overline{x}} - e^{-\lambda_+ \overline{x}} \right) \right) \right) \\ \leqslant C\, K w(0)^{-\frac{\alpha}{\lambda_-}}, \end{aligned}$$

where $C > 0$ is a universal constant.

We consider now the case where the maximum of $\tilde{w}$ is reached on the set $[-\infty, 0) \setminus \{x \in \mathbb{R};\ \underline{w}(x) \leqslant 3/4 - K\}$. If this supremum is a maximum attained in $\bar{x}$, then $\overline{w}(\bar{x}) + \underline{w}(\bar{x}) \geq \frac{3}{2} - 2K > 1$ (this last inequality holds if K is small enough), and $-c\tilde{w}'(\bar{x}) - \tilde{w}''(\bar{x}) \geqslant 0$, which implies

$$(\overline{w} + \underline{w} - 1)\tilde{w}(\overline{x}) \leqslant K + 2K\underline{w} \leqslant K(3 - 4K),$$

that is $\tilde{w}(\overline{x}) \leqslant \frac{K(3-4K)}{1/2-2K} \leq CK$ for some constant $C > 0$, provided $K > 0$ is small enough. If the supremum is not a maximum, it is possible to obtain a similar estimate, we skip here the additional technical details.

We have shown that

$$\sup_{[-\infty,0]} \tilde{w} \leq \max\left(CK, CKw(0)^{-\frac{\alpha}{\lambda_-}}\right),$$

We choose now $\beta = (1 + \alpha/\lambda_-)^{-1} \in (0, 1/2)$ and $w(0) = K^\beta$ (we recall that the solution (c, w, m) is still a solution when w and m are translated). Then, $\sup_{[-\infty,0]} \tilde{w} \leqslant CK^\beta$, and thus

$$\|w - u\|_{L^\infty((-\infty,0])} \leqslant \|\tilde{w}\|_{L^\infty((-\infty,0])} \leqslant CK^\beta.$$

Furthermore, w and u are decreasing for $x \geqslant 0$ thanks to Proposition 2.5.1, which implies that

$$\forall x \geqslant 0, |w - u|(x) \leqslant w(x) + u(x) \leqslant w(0) + u(0) \leqslant 2K^\beta.$$

From [108, Theorem 8.33], there exists a universal constant that we denote $C > 0$ such that

$$\|v\|_{C^{1,\alpha}} \leqslant C, \tag{2.32}$$

where v is a solution of (2.6), and this constant C is uniform in the speed c in the neighbourhood of $c_0 = 2\sqrt{r}$. In particular, u satisfies

$$-c_0u' - u'' = (c_* - c_0)u' + u(1 - u) = u(1 - u) + \mathcal{O}(K). \tag{2.33}$$

Let v the solution of (2.6) with speed c_0 and $v(0) = u(0)$, the above argument can then be reproduced to show that

$$\|u - v\|_{L^\infty} \leq CK^\beta, \tag{2.34}$$

where C is a universal constant and β depend only on r, which finishes the proof. □

2.6 Appendix

2.6.1 Compactness results

We provide here two results that are used in the proof of Theorem 2.2.1.

Lemma 2.6.1 (Elliptic estimates)**.** *Let* a, b^-, $b^+ \in \mathbb{R}_+^*$, $g \in L^\infty(-a,a)$, *and* $\gamma > 0$. *For any* $b^+, b^- \in \mathbb{R}$ *and* $c \in [-\gamma, \gamma]$, *the Dirichlet problem*

$$\begin{cases} -cw' - w'' = g, \quad (-a,a), \\ w(-a) = b^-,\ w(a) = b^+, \end{cases}$$

has a unique weak solution w. *In addition we have* $w \in C^{1,\alpha}([-a,a])$ *for all* $\alpha \in [0,1)$, *and there is a constant* $C > 0$ *depending only on* a *and* γ *such that*

$$\|w\|_{C^{1,\alpha}([-a,a])} \leqslant C(\max(|b^+|, |b^-|) + \|g\|_{L^\infty}),$$

Proof of Lemma 2.6.1. As the domain lies in $\mathbb{R}$, we are not concerned with the regularity problem near the boundary. Since

$$L^\infty(-a,a) \subset \bigcap_{p>1} L^p(-a,a),$$

thanks to [108, Theorem 9.16] we have existence and uniqueness of a solution $w \in W^{2,p}$, for all $p > 1$. We deduce from Sobolev imbedding that $w \in C^{1,\alpha}([-a,a])$ for all $\alpha < 1$.

The classical theory [108, Theorem 3.7] gives us a constant $C' > 0$ depending only on a and γ such that

$$\|w\|_{L^\infty} \leqslant \max(b^+, b^-) + C'\|g\|_{L^\infty}.$$

The estimate on the Hölder norm of the first derivative comes now from [108, Theorem 8.33], which states that whenever w is a $C^{1,\alpha}$ solution of $-cw' - w'' = g$ with $g \in L^\infty$, then

$$\|w\|_{C^{1,\alpha}([-a,a])} \leqslant C''(\|w\|_{C^0([-a,a])} + \|g\|_{L^\infty}),$$

with a constant $C'' = C''(a,\gamma)$ depending only on a and γ. That proves the theorem. $\square$

Lemma 2.6.2. *Let* a, b^-, $b^+ \in \mathbb{R}_+^*$. *The operator* $(L)_D^{-1} : \mathbb{R} \times C^0([-a,a]) \to C^0([-a,a])$ *defined by*

$$L_D^{-1}(c,g) = w,$$

where w *is the unique solution of*

$$\begin{cases} -cw' - w'' = g, \quad (-a,a), \\ w(-a) = b^+, w(a) = b^-, \end{cases}$$

is continuous and compact.

Proof of Lemma 2.6.2. Let $(c,g),(\tilde{c},\tilde{g}) \in \mathbb{R}\times C^0([-a,a])$, $\gamma>0$ and $w,\tilde{w}\in C^0([-a,a])$ such that $c,\tilde{c}\leqslant\gamma$ and

$$\begin{cases} -cw' - w'' = g \text{ on } (-a,a), \\ w(-a) = b^+, w(a) = b^-, \end{cases}$$

$$\begin{cases} -\tilde{c}\tilde{w}' - \tilde{w}'' = \tilde{g} \text{ on } (-a,a), \\ \tilde{w}(-a) = b^+, \tilde{w}(a) = b^-. \end{cases}$$

Then $w-\tilde{w}$ satisfies

$$\begin{cases} -c(w-\tilde{w})' - (w-\tilde{w})'' = g - \tilde{g} + (c-\tilde{c})\tilde{w}' \text{ on } (-a,a), \\ (w-\tilde{w})(-a) = 0, (w-\tilde{w})(a) = 0. \end{cases}$$

We deduce from Lemma 2.6.1 that there exists a constant C depending only on $a>0$ such that

$$\|w-\tilde{w}\|_{C^0} \leqslant C(\|g-\tilde{g}\|_{C^0} + |c-\tilde{c}|(\|\tilde{g}\|_{C^0} + \max(b^+,b^-))),$$

which shows the pointwise continuity of L_D^{-1}.

Now let (c_n,g_n) a bounded sequence in $\mathbb{R}\times C^0$. Let $\gamma = \limsup|c_n|$. From Lemma 2.6.1 we deduce the existence of a constant $C>0$ depending only on a and γ such that

$$\|u_n\|_{C^1} \leqslant C(\max(b^+,b^-) + \|g_n\|_{C^0}),$$

where $u_n = L_D^{-1}(c_n,g_n)$, which shows that (g_n) is bounded in C^1. Since C^1 is compactly embedded in C^0, there exists a $w\in C^0$ such that $\|u_n - w\|_{C^0}\to 0$. This shows the compactness of L_D^{-1}. □

2.6.2 Properties of the reaction terms

The proofs of Theorem 2.2.2 requires precise estimates on the reaction terms f^w and f^m. Here we prove a number of technical lemmas that are necessary for our study.

Lemma 2.6.3. *Let r, K, μ satisfy Assumption 2.1.1, and ϕ_w, ϕ_m defined by* (2.22) *and* (2.23) *respectively. Then, ϕ_w, $\phi_m : \mathbb{R}_+ \to \mathbb{R}$ are decreasing functions such that*

$$\phi_w([0,K]) \subset (\mu,\infty), \quad \phi_m([0,1]) \subset (\mu K/r,\infty).$$

Proof of Lemma 2.6.3. We prove the lemma for ϕ_m. The results on ϕ_w follow since both functions coincide when $r=K=1$. The fact that ϕ_m is decreasing simply comes from the computation of its derivative:

$$\phi_m'(w) = \frac{1}{2}\left[-1 + \frac{-2\left(K - \frac{\mu K}{r} - w\right) + 4\frac{\mu K}{r}}{2\sqrt{\left(K - \frac{\mu K}{r} - w\right)^2 + 4\frac{\mu K}{r}w}}\right],$$

one can check that $\phi_m'(w) < 0$ for all $w \geq 0$ as soon as $\mu < \frac{r}{2}$. Next, we can estimate $\phi_m(w)$ for $w > 0$ large:

$$\begin{aligned}
\phi_m(w) &= \frac{w + \frac{\mu K}{r} - K}{2}\left(-1 + \sqrt{1 + \frac{4\mu K w}{r\left(w + \frac{\mu K}{r} - K\right)^2}}\right) \\
&= \frac{w + \frac{\mu K}{r} - K}{2}\left(\frac{2\mu K w}{r\left(w + \frac{\mu K}{r} - K\right)^2} + o(1/w)\right) \\
&= \frac{\mu K}{r} + o(1),
\end{aligned}$$

that is $\lim_{w\to\infty} \phi_m(w) = \frac{\mu K}{r}$, which, combined to the variation of ϕ_w, shows that $\phi_m([0,1]) \subset (\mu K/r, \infty)$. □

Lemma 2.6.4. *Let r, K, μ satisfy Assumption 2.1.1, ϕ_w, ϕ_m defined by (2.22) and (2.23) respectively.*

$$Z_w = \{(w,m) \in (0,1) \times (0,K) / f^w(w,m) = 0\},$$

$$Z_m = \{(w,m) \in (0,1) \times (0,K) / f^m(w,m) = 0\},$$

and denote

$$\mathcal{D} = (0,1) \times (0,K). \tag{2.35}$$

Then:

1. *Z_w can be described in two ways:*

$$Z_w = \{(\phi_w(m), m)\,, m \in (0,K)\}\,, \tag{2.36}$$

and

$$Z_w = \{(w, \varphi_w(w))\,, w \in (\mu,1)\} \cap \mathcal{D}, \tag{2.37}$$

where $\varphi_w(w) = \frac{w(1-\mu-w)}{w-\mu}$.

2. *Similarly, Z_m can be described as:*

$$Z_m = \{(w, \phi_m(w))\,, w \in (0,1)\}\,, \tag{2.38}$$

and

$$Z_m = \left\{(\varphi_m(m), m)\,, m \in \left(\frac{\mu K}{r}, K\right)\right\} \cap \mathcal{D}, \tag{2.39}$$

where $\varphi_m(m) := \frac{m(K - \frac{\mu K}{r} - m)}{m - \frac{\mu K}{r}}$.

Proof of Lemma 2.6.4. Notice that point 1 can be obtained from point 2 by setting $r = K = 1$. Thus, we are only going to prove point 2. We write

$$f^m(w,m) = rm\left(1 - \frac{w+m}{K}\right) + \mu(w-m) = -\frac{r}{K}m^2 + \left(r - \mu - \frac{r}{K}w\right)m + \mu w.$$

Since $\Delta = \left(r - \mu - \frac{r}{K}w\right)^2 + 4\frac{\mu r}{K}w > 0$ for any $w \geq 0$, $f^m(w,m) = 0$ admits only two solutions for $w \geq 0$ fixed. Those write:

$$\frac{1}{2}\left((K - \frac{\mu K}{r} - w) \pm \sqrt{(K - \frac{\mu K}{r} - w)^2 + 4\frac{\mu K}{r}w}\right),$$

one of those two solutions is negative for all $w \neq 0$, so that $f^m(w,m) = 0$ with $(w,m) \in \mathcal{D}$ implies that $m = \phi_m(w)$, which leads to (2.38).

Thanks to Lemma 2.6.3, $m > \mu K/r$ on Z_m, $f(w,m) = 0$ with $(w,m) \in \mathcal{D}$ then implies $w = \varphi_m(m)$. For $m \in \left(0, \frac{\mu K}{r}\right)$, $\varphi_m(m)$ is decreasing and

$$\begin{cases} \varphi_m(0) = 0, \\ \lim\limits_{m \to \left(\frac{\mu K}{r}\right)^-} \varphi_m(m) = -\infty, \end{cases}$$

so that $\varphi_m(m) < 0$ for $m \in \left(0, \frac{\mu K}{r}\right)$. That proves (2.39). □

The next lemma proves that f admits only one zero in $\mathcal{D}$, and proves some inclusions between $f^m > 0$ and $f^w > 0$.

Lemma 2.6.5. *Let r, K, μ satisfy Assumption 2.1.1, ϕ_w, ϕ_m, φ_w, φ_m defined by* (2.22), (2.23), (2.37) *and* (2.39) *respectively. Then ϕ_w and φ_m are convex, strictly decreasing functions over* $(0, K)$ *and* $\left(\frac{\mu K}{r}, K\right)$ *respectively.*

Proof of Lemma 2.6.5. We have already shown that ϕ_w is decreasing on $(0, K)$. We compute:

$$\phi_w'(m) = -\frac{1}{2}\left(1 + \frac{1 - 3\mu - m}{\sqrt{(1-\mu-m)^2 + 4\mu m}}\right).$$

Computing the second derivative, we find:

$$\begin{aligned} \phi_w''(m) &= \frac{(1-\mu-m)^2 + 4\mu m - (1-3\mu-m)^2}{2\left((1-\mu-m)^2 + 4\mu m\right)^{\frac{3}{2}}} \\ &= \frac{2\mu(1-2\mu)}{\left((1-\mu-m)^2 + 4\mu m\right)^{\frac{3}{2}}} > 0, \end{aligned}$$

so that ϕ_w is convex over $\mathbb{R}_+$. Thanks to polynomial arithmetics, we compute:

$$\varphi_m(m) = \frac{m\left(K\left(1-\frac{\mu}{r}\right)-m\right)}{m-\frac{\mu K}{r}} = K\left(1-\frac{2\mu}{r}\right) - m + \frac{\frac{\mu K^2}{r}\left(1-\frac{2\mu}{r}\right)}{m-\frac{\mu K}{r}},$$

which makes φ_m obviously convex and strictly decreasing on $\left(\frac{\mu K}{r}, K\right)$. $\square$

Lemma 2.6.6. *There exists a unique solution to the problem:*

$$f^w(w,m) = f^m(w,m) = 0, \tag{2.40}$$

with $(w,m) \in (0,1) \times (0,K)$.

Proof of Lemma 2.6.6. We write:

$$f^w = w(1-\mu-w) + m(\mu-w).$$

Since $\mu < \frac{1}{2}$, we have

$$f^w(\mu,m) = \mu(1-2\mu) > 0,$$

so that there cannot be a solution of $f^w(w,m) = 0$ with $w = \mu$. Thus, $f^w(w,m) = 0$ if and only if

$$m = \frac{w(1-\mu-w)}{w-\mu}. \tag{2.41}$$

Substituting (2.41) in $f^m(w,m) = 0$, we get:

$$(2.40) \Rightarrow \underbrace{r\frac{w(1-\mu-w)}{w-\mu}\left(1-\frac{\frac{w(1-\mu-w)}{w-\mu}+w}{K}\right)}_{A} + \mu\underbrace{\left(w-\frac{w(1-\mu-w)}{w-\mu}\right)}_{B} = 0.$$

We compute:

$$A = \frac{rw(1-\mu-w)}{K(w-\mu)^2}\left(w(K+2\mu-1)-\mu K\right),$$

$$B = \mu\frac{w(2w-1)}{w-\mu}.$$

From now on we assume $w \neq 0$. Then:

$$(2.40) \Rightarrow C(w) := \frac{r}{K}(1-\mu-w)(w(K+2\mu-1)-\mu K)+\mu(2w-1)(w-\mu) = 0.$$

Now C is a polynomial function of degree at most 2. We compute:

$$C(0) = \mu(1 - r(1-\mu)) < 0,$$

$$C(1) = \mu\left(1 - \mu + \frac{r}{K}((1-\mu)(1-K) - \mu)\right) > 0,$$

under the following assumptions:

$$\mu < 1 - \frac{1}{r},$$

$$K < \frac{r}{r-1}\left(1 - \frac{\mu}{1-\mu}\right).$$

That proves the uniqueness of a solution of (2.40) with $w \in (0,1)$.

Now recall the notations of lemmas 2.6.4 and 2.6.5. The existence of a solution to problem (2.40) is equivalent to showing $Z_m \cap Z_w \neq \varnothing$. Since:

$$\Phi_w\left(\frac{\mu K}{r}\right) \in \mathbb{R},$$

$$\lim_{m \to \left(\frac{\mu K}{r}\right)^+} \varphi_m(m) = +\infty,$$

$$\Phi_w(K) = \frac{1}{2}\left(1 - \mu - K + \sqrt{(1-\mu-K)^2 + 4\mu K}\right) > 0,$$

$$\varphi_m(K) = -\frac{\mu}{r-\mu} < 0,$$

and since Φ_w and φ_m are continuous over $\left(\frac{\mu K}{r}, K\right)$, there exists a solution to $\varphi_m(m) = \Phi_w(m)$ with $m \in \left(\frac{\mu K}{r}, K\right)$.

Since $\forall m \in (0,K), 0 < \Phi_w(m) < 1$, that gives us a solution to (2.40), and proves Lemma 2.6.6. $\square$

Lemma 2.6.7. *Let* $\mathcal{D} = (0,1) \times (0,K)$,

$$\begin{aligned}
Z_w &= \{f^w = 0\} \cap \mathcal{D} = \{w = \phi_w(m)\} \cap \mathcal{D} \\
Z_w^- &= \{f^w < 0\} \cap \mathcal{D} = \{w > \phi_w(m)\} \cap \mathcal{D}, \\
Z_m &= \{f^m = 0\} \cap \mathcal{D} = \{m = \phi_m(w) = 0\} \cap \mathcal{D}, \\
Z_m^- &= \{f^m < 0\} \cap \mathcal{D} = \{m > \phi_m(w) < 0\} \cap \mathcal{D},
\end{aligned}$$

and

$$\mathcal{D}_l = \{(w,m) \in \mathcal{D}, w \leq w^*, m \geq m^*\},$$

$$\mathcal{D}_r = \{(w,m) \in \mathcal{D}, w \geq w^*, m \leq m^*\},$$

where (w^*, m^*) *is the only solution of* $f^m = f^w = 0$ *in* $\mathcal{D}$*. Then*

$$Z_m \cup Z_w \subset \mathcal{D}_l \cup \mathcal{D}_r. \tag{2.42}$$

Moreover,

$$Z_w^- \cap \mathcal{D}_l \subset Z_m^-, \tag{2.43}$$

$$Z_m^- \cap \mathcal{D}_r \subset Z_w^-. \tag{2.44}$$

Remark 2.6.8. Let

$$Z_w^+ = \{f^w > 0\} \cap \mathcal{D} = \{w < \phi_w(m)\} \cap \mathcal{D},$$
$$Z_m^+ = \{f^m > 0\} \cap \mathcal{D} = \{m < \phi_m(w)\} \cap \mathcal{D}.$$

Lemma 2.6.7 implies that

$$Z_m^+ \cap \mathcal{D}_l \subset Z_w^+, \quad Z_w^+ \cap \mathcal{D}_r \subset Z_m^+.$$

Proof of Lemma 2.6.7. Assertion (2.42) comes from the fact that Φ_w and φ_m are decreasing.

Assertion (2.43) comes from the fact that $\Phi_w - \varphi_m$ is negative for m close to $\left(\frac{\mu K}{r}\right)^+$ and does not change sign in $\left(\frac{\mu K}{r}, m^*\right)$ since (w^*, m^*) is the only solution of (2.40). A similar argument proves assertion (2.44) □

The last thing we need here is an estimate of the behaviour of $m^*(\mu, r, K)$ when $\mu \to 0$:

Lemma 2.6.9. *For* $\mu < 1 - K$*, we have*

$$m^*(\mu, r, K) \leq \frac{\frac{\mu K}{r}(1-\mu)}{1 - \mu - K\left(1 - \frac{2\mu}{r}\right)}. \tag{2.45}$$

Proof of Lemma 2.6.9. Recall the notations of Lemma 2.6.5. From Lemma 2.6.6 we know that m^* is the only solution of $\Phi_w = \varphi_m$ that lies in $(0, K)$. Since $m \mapsto \sqrt{m}$ is increasing and $1 - \mu - K > 0$, we have:

$$\Phi_w(m) \geq 1 - \mu - m. \tag{2.46}$$

We deduce then:

$$\varphi_m(m) - \Phi_w(m) \leq \varphi_m(m) - (1 - \mu - m).$$

Now $\varphi_m - \Phi_w$ is positive near $\left(\frac{\mu K}{r}\right)^+$, and for $w \in \left(\frac{\mu K}{r}, m^*\right)$,

$$0 < \varphi_m(w) - \Phi_w(w) \leq \varphi_m(w) - (1 - \mu - m),$$

which means that if $\bar{m}$ satisfies

$$\varphi_m(\bar{m}) = 1 - \mu - \bar{m}. \tag{2.47}$$

then $\bar{m} \geq m^*$. A simple computation shows that the only solution of (2.47) is:

$$\bar{m} = \frac{\frac{\mu K}{r}(1-\mu)}{1 - \mu - K\left(1 - \frac{2\mu}{r}\right)},$$

which finishes to prove Lemma 2.6.9 $\square$

Chapitre 3

Virulence evolution at the front line of spreading epidemics

3.1 Introduction

The emergence of infectious diseases is an ever increasing source of concern for human health, agriculture and wildlife conservation. Understanding the epidemiological dynamics of pathogen populations may help limit the potentially devastating consequences of epidemics for animal and plant species. For instance, it is particularly important to understand which factors govern the speed of epidemics to predict and potentially prevent the spatial spread of pathogens. Historical reports allow estimating the speed of various epidemics like the the Black Death in the 14th century (320-650km/year) or rabies in Europe in the last century (30-60 km/year) [188]. More recently, several studies indicate that the speed of epidemics is not constant but can accelerate with time [158]. Even more complex spatio-temporal patterns have been described in measles spreading in heterogeneous host populations [112]. Is it possible to understand what governs this diversity of invasion patterns from one disease to another?

Determining the speed of biological invasions has attracted a lot of attention from theoretical biologists [89, 190, 141]. Under the simplifying assumption that the environment is homogeneous and that the kernel of dispersal is normally distributed, diffusion models can be used to predict the asymptotic speed of the spatial spread of the population [89, 143, 188]. Typically, the population spreads as a traveling wave with a speed equal to $2\sqrt{\sigma r}$, where r is the exponential growth rate of the population at low density and σ is the diffusion coefficient which measures how quickly the organisms disperse [188]. Relaxing the underlying assumptions of this model may alter quantitatively the speed of the travelling wave. For instance, adding spatial and/or temporal heterogeneity in the environment may speed up or slow down (depending on which parameter is affected by the environment) the invasion [188, 187, 80]. Modifying the shape of the dispersal distribution may have even more dramatic consequences on the invasion dynamics. In particular, fat-tailed kernels of dispersal can generate accelerating invasions rather than constant-speed traveling waves [143, 188].

Previous studies have mostly focused on the spatial dynamics of invasions under the assumption that evolutionary dynamics could be neglected because it is a much slower process [164]. There is overwhelming evidence, however, that evolution is often very rapid during invasions [165]. In particular, spatial sorting drives dispersal evolution at the invasion front and may result in the accumulation of individuals with extreme dispersal abilities at its edge. This spatial sorting of phenotypes [189] may also act on other phenotypic traits. Indeed, the edge of the front is characterized by low density dependence and may select for higher growth rates [166, 54]. Because selection for higher σ and higher r is expected to affect propagation speed, rapid evolution may be another factor that could generate accelerating invasions [164, 165]. Pathogens are likely to exhibit rapid evolution during an epidemic. Viral populations, in particular, are often characterized by large population sizes and large mutation rates which may fuel the genetic variability of pathogen populations [132]. This genetic variability implies that epidemiological and evolutionary processes occur simultaneously. Evolutionary epidemiology theory tracks the transient dynamics of pathogens during epidemics taking place in well-mixed environments [72, 70, 30]. The influence of spatial structure on the ultimate evolution of virulence has been examined in several earlier studies [40, 148, 147]. But most of those studies focused on the long term evolution of the pathogen after it has reached an endemic equilibrium. Wei and Krone [201], in contrast, studied the emergence of mutant pathogens in phage epidemics spreading in a lawn of susceptible bacteria. They pointed out that the invasion success of a mutant pathogen depends on the life history traits of the mutant and the location of the mutant relative to the front of the epidemic. More recently, Osnas et al [161] studied the interplay between the pathogen's virulence and its influence on the host's ability to disperse. In their model the wave of the epidemic can be invaded by a low virulence strain, which diffuses faster, and is followed by an intermediate virulence strain before reaching the evolutionary equilibrium. Here we extend previous studies and follow epidemiology and evolution during the spatial spread of an epidemic. We develop a model based on reaction-diffusion equations to understand virulence evolution and its impact on the speed of an epidemic taking place in a homogeneous host population. This deterministic model shows how mutation can affect the epidemiological dynamics and speed up the spatial spread of a pathogen. We explore the robustness of these conclusions in various epidemiological

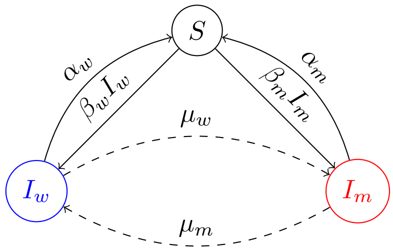

Figure 3.1 – Schematic representation of the pathogen life cycle. Arrows represent the transitions between states. The label indicate the rates at which those transitions occur.

scenarios under a broad range of pathogen life cycles. Finally, we confront these analytical results with individual-based simulations and explore the impact of demographic stochasticity on invasion dynamics.

3.2 Model

Epidemiology and evolution

We use a classical epidemiological model where the host can either be susceptible or infected. We assume that two pathogen genotypes are circulating in the host population: a wild type genotype (w) and a mutant genotype (m). Coinfections with the two genotypes are not allowed. Each genotype i ($i \in \{w, m\}$) is characterised by two specific life history traits. First, β_i is the rate at which transmission occurs between infected and susceptible hosts after a contact. Second, α_i is the mortality rate of infected hosts. Mutation may occur between these two genotypes and μ_i stands for the rate of mutation from genotype i to the other genotype (see Figure 3.1). The transmission of the pathogen is assumed to be local (infected hosts can only infect susceptible hosts at the same spatial location) but both susceptible and infected hosts are allowed to diffuse in one dimension with a fixed rate σ. In other words we neglect the influence the pathogen may have on the mobility of its hosts. The densities of the different types of host at location x and time t are noted $S(x,t)$ (susceptible hosts) and $I_i(x,t)$ (infected hosts with genotype i). For the sake of simplicity we assume that dead hosts are immediately replaced by new susceptible hosts. Consequently the total host population size is assumed to remain constant and equal to $N = S(x,t) + I_w(x,t) + I_m(x,t)$. Our model can thus be written as a set of reaction-diffusion equations (for readability we drop the time and space dependence notation in the following):

$$\begin{cases} \frac{\partial I_w}{\partial t} = \sigma \frac{\partial^2 I_w}{\partial x^2} + r_w I_w \left(1 - \frac{I_w + I_m}{K_w}\right) + \mu_m I_m - \mu_w I_w \\ \frac{\partial I_m}{\partial t} = \sigma \frac{\partial^2 I_m}{\partial x^2} + r_m I_m \left(1 - \frac{I_w + I_m}{K_m}\right) + \mu_w I_w - \mu_m I_m \end{cases} \tag{3.1}$$

with $r_i = \beta_i - \alpha_i$ and $K_i = N\left(1 - \frac{\alpha_i}{\beta_i}\right) = N\left(1 - \frac{1}{R_{0,i}}\right)$ (see derivation in the SI, section 3.5.1). In the following we focus on situations where $r_i > 0$, meaning that both pathogens have the ability of producing an epidemic. With these assumptions, r_i can be interpreted as a growth rate and K_i as a carrying capacity for each respective strain. In the SI (section 3.5.10), we provide more information concerning the link between the epidemiological parameters α and β, and the ecological ones r and K. Note that $R_{0,i} = \frac{\beta_i}{\alpha_i}$ measures the basic reproductive ratio of genotype i. It can be shown that if we assume $r_i > r_j$ and $K_i > K_j$ strain j is outcompeted by strain i throughout the habitat.

In addition we assume that $r_m > r_w$ and $K_w > K_m$. In other words we are considering a situation where a wild type genotype can give rise to a virulent genotype by mutation. Increased virulence is detrimental to pathogen fitness (notice that $K_m < K_w$ is equivalent to $R_{0,m} < R_{0,w}$) but we assume that this mutation has a pleiotropic effect and is associated with an increased transmission rate. Our hypothesis can be reformulated in terms of epidemiological parameters : given a wild type phenotype (β_w, α_w), an admissible mutant has a phenotype (β_m, α_m) satisfying the constraint : $\beta_m < \alpha_m R_{0,w}$ and $\beta_m > (\beta_w - \alpha_w) + \alpha_m$. This is a classical scenario considered to understand the evolution of pathogen virulence [93, 8]. The originality of the present model is to study this joint epidemiological and evolutionary dynamics in a spatially explicit context.

3.3 Results

Epidemic speed

Numerical solutions of (3.1) have a distinctive shape represented in Figure 3.2, that proves to be very robust under a broad range of parameter values. The mutant genotype is always present at the front because it has a higher instantaneous rate of growth r_m. Away from the front, however, the wild type genotype outcompetes the mutant genotype because it has a higher carrying capacity K_w (i.e. the wild type has a higher basic reproductive ratio $R_{0,w}$). Using a linear approximation near the edge of the front, we obtain an analytical expression for the speed (presented in (3.2) ; see also SI section 3.5.2) of the travelling waves associtated with equation (3.1).

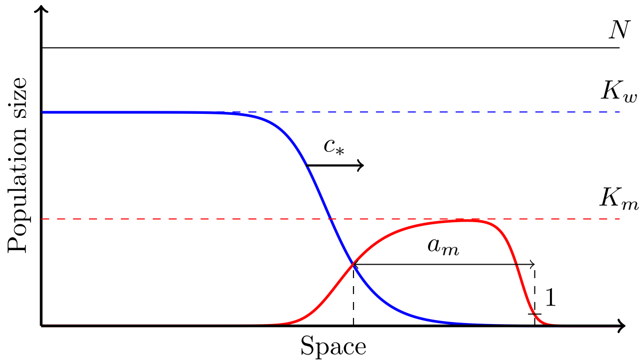

Figure 3.2 – Shape of the stationary front of the spreading epidemic. The epidemic moves at a constant speed c^*. The mutant genotype (in red) is prevalent at the edge of the front and reaches a maximal density of K_m. Behind the front, the wild type genotype (in blue) takes over and reaches a higher density K_w. The size of the area where the mutant is more abundant that the wild type is called the mutant's range, a_m.

$$\begin{aligned} c^* = \quad & \sqrt{2\sigma}\Big(r_w + r_m - (\mu_w + \mu_m) \\ & + \sqrt{(r_m - r_w)^2 + 2(r_w - r_m)(\mu_m - \mu_w) + (\mu_w + \mu_m)^2}\Big)^{\frac{1}{2}} \end{aligned} \tag{3.2}$$

When both μ_w and μ_m are assumed to be small the speed of the epidemic reduces to:

$$c^* = c_m - \kappa(\mu_w, \mu_m) + o(\mu_w, \mu_m) \tag{3.3}$$

where $c_m = 2\sqrt{\sigma r_m}$ is the deterministic speed of the mutant alone, and κ is a linear function representing the mutation load on the speed:

$$\kappa(\mu_w, \mu_m) = \mu_m \sqrt{\frac{\sigma}{r_m}}$$

In other words the spatial dynamics of the whole epidemic is mainly driven by the mutant genotype. In particular it is driven by its instantaneous growth rate r_m. When an epidemic starts from a population composed only of wild type, it will at first behave like the wild type and experience a transitory phase before reaching the behavior of a traveling wave. We did a brief presentation of these transitory dynamics in the SI, section 3.5.3.

Mutant's range

To better characterize the front of the epidemic we derive an approximation for the size of the area a_m where the mutant is abundant (Figure 3.2). This approximation is based on a set of simplifying assumptions to capture the

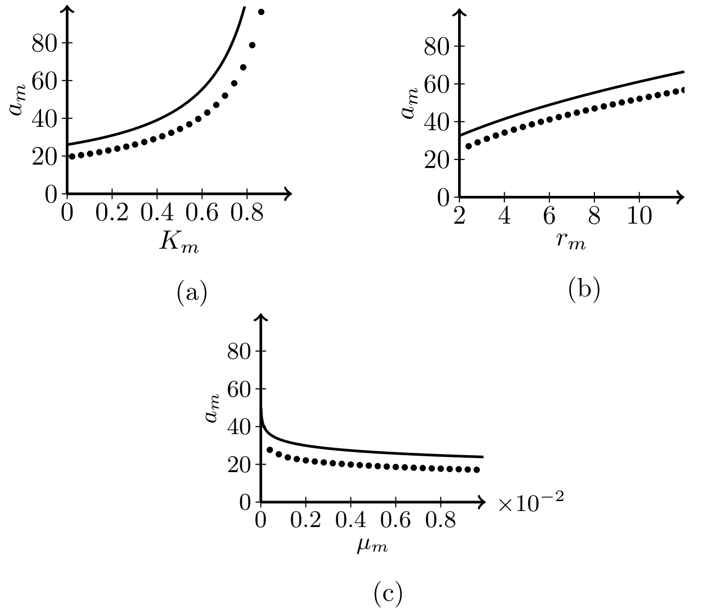

Figure 3.3 – Effects of K_m, r_m and μ_m on the size of the mutant's range a_m in (a), (b) and (c), respectively. The full lines present the approximation given in (3.4). The dots present the mutant's range obtained from numerical simulations at time $t = 500$.

main steps of the competition going on during the invasion. First, we assume that one mutant is introduced and grows exponentially to carrying capacity with rate r_m. When the mutant reaches its carrying capacity K_m the wild type is introduced at rate μ_m from the population of mutants and grows at rate r_w until its density becomes higher than K_m (see section 3.5.4 of the SI for the derivation). The approximation for the mutant's range is defined as the spatial distance between the tip of the front and the point where the density of the wild type becomes higher than the mutant's:

$$a_m \approx 2\sqrt{\frac{\sigma}{r_m}} \log\left(K_m\right) - \frac{2\sqrt{\sigma r_m}}{\left(1 - \frac{K_m}{K_w}\right) r_w} \log \mu_m \tag{3.4}$$

This expression captures the effect of several parameters. In particular the mutant's range increases with r_m and K_m which measure the competitive ability of the mutant at the tip of the front and behind the front, respectively. As expected the mutant's range decreases when the influx μ_m of wild type genotypes increases. Figure 3.3 shows that this approximation agrees well with the mutant's range derived from numerical solutions of equation (3.4).

Mutation-selection equilibrium behind the front

The above results characterize the speed and the shape of the front. Behind the front the wild type genotype outcompetes the mutant but mutation μ_w can reintroduce the mutant in the pathogen population. The equilibrium density of the mutant results from the balance between mutation and selection. Under the assumptions that mutation rates remain low relative to the growth rates and that the pathogen population is equal to K_w we recover a classical result from population genetics [66] on the equilibrium frequency (see SI section 3.5.5):

$$p_{eq} \approx \frac{\mu_w}{s} \tag{3.5}$$

where s measures the selection against the mutant at the endemic equilibrium (for more information about s, see section 3.5.5 in the SI). It is worth noting that the mutation load behind the front is mainly governed by the mutation rate μ_w while the mutation load on the speed of the epidemic is mainly driven by μ_m (see (3.3)). This is because selection varies between the edge of the front (where the mutant is selected for) and behind the front (where the mutant is selected against).

Alternative epidemiological models

Our model relies on the assumption that dead hosts are immediately replaced by susceptible ones and that infected hosts cannot recover from the infection. We relaxed these assumptions and analysed the epidemiology and evolution under alternative epidemiological models. First, we examined a situation where there is no host reproduction (see details in the SI, section 3.5.6). This model may be relevant to describe the spatial spread of a bacteriophage on a bacterial lawn [201]. When lytic bacteriophages spread, the burst of bacterial cells release new virions but rapidly exhausts the resource (i.e. host density drops) behind the front. Yet, when a virulent strain is allowed to appear by mutation we recover the profile described above (Figure 3.7).

We also examined a situation where the infected hosts can recover and become immune to the infection (see details in the SI, section 3.5.6). Here, again, we recover the same qualitative result (Figure 3.8) where the mutant is at the edge of the front and it is replaced by the wild type. The main difference between these two scenarios and the simpler SI model analysed before is the drop in the density of the wild type behind the front. Note that this drop may be characterized in the second scenario by damped oscillations when recovery rates are large [188].

These alternative models do not alter qualitatively our results because these modifications of pathogen's life cycle do not affect processes going on at the edge of the front. In particular, the formula for the speed remains valid.

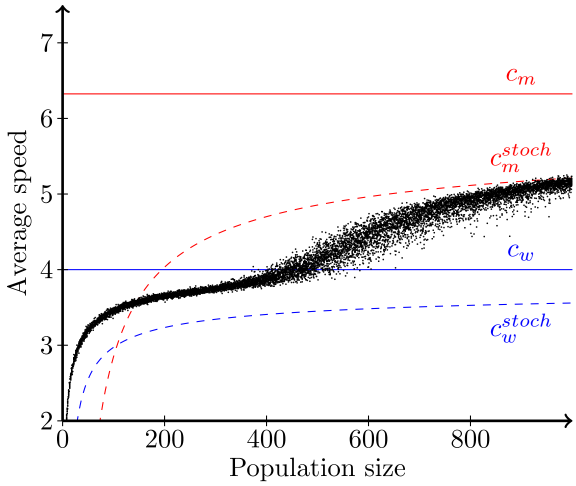

Figure 3.4 – Effect of host population size N on the average speed of the stochastic epidemic. 100 simulations were done for each value of N and each dot represents the average epidemic speed for a single simulation, taken between time $t = 200$ and $t = 1000$.

However, the specific structure of Equation (3.1) is only valid as a first-order approximation near the edge of the front in thoses cases. This is true for the formula of K, which may no longer correspond to the carrying capacity in the back of the front. Other modifications of the life cycle can have a more profound impact on evolutionary dynamics. For instance Osnas et al [161] assumed that infected hosts have a lower tendency to disperse. This selects for lower virulence at the front of the epidemic. In all those scenarios, however, the parasite strain taking over at the edge of the front are the ones characterised with the fastest rate of spread of the epidemic wave.

Stochastic simulations

The above results are derived from a fully deterministic model. We explored the effect of stochasticity using an individual-based model that takes into account that the number N of hosts per site is finite and h measures the spatial distance between sites. As above, hosts can be in three states : susceptible, infected by a wild type pathogen or infected by a mutant pathogen. The individual transitions between these states are described by a list of random events (transmission, mutation, death ; see Figure 3.1 and SI section 3.5.7 for a detailed description). This stochastic model converges to the above deterministic model (3.1) when N is assumed to be very large.

In order to catch the front dynamics, we performed simulations with our individual-based model and measured the average speed on a long period after the influence of the initial condition is lost. These simulations show that the asymptotic speed of the epidemic depends on the number of individuals per unit of space. A lower host population size reduces the speed of the front. This effect is due to the stochasticity occuring at the edge of the front. In contrast with the deterministic model, the density at the front cannot fall below $1/N$ (it takes at least 1 infected host over the N possible hosts to create a front). This discreteness affects the shape of the front and, consequently, the speed of the travelling wave. Following [51] and [157], we obtained an approximation that captures the effect of finite population size on the speed of the front (see details in the SI, section 3.5.8) :

$$c_i^{stoch} \approx c_i - \sqrt{\sigma r_i} \left(\frac{\pi}{\log\left(\frac{K_i}{h}\right)} \right)^2$$

This estimate matches the qualitative asymptotic behaviour of the speed, and becomes increasingly accurate as h goes to zero (recall that h measures the distance between sites and π is the mathematical constant). Figure 3.4 shows that the match between this approximation and the simulation is not very good when population size gets very low. Yet the approximation captures the qualitiative effect of finite population size. In particular we see that the speed of the mutant is more affected by finite population size. There is a critical population size below which the front of the mutant is slower than the front of the wild type. In that situation the mutant cannot invade and the epidemic is driven by the wild type genotype. When population size increases there is a region where the front oscillates between the wild type and the mutant. When the mutant manages to be at the front, the speed increases (see Figure 3.9) but the mutant can get lost stochastically due to genetic drift. For larger population sizes the mutant can remain at the front for longer periods of time and the speed of the traveling wave increases. As expected, for infinitely large host populations, the speed of the epidemic converges to c^*.

We also developed a two-dimensional version of our stochastic simulation model. Figure 3.5 presents the results under different scenarios. This figure illustrates the impact of the initial condition and the strength of selection on (i) the genotypic diversity in a growing epidemic, (ii) the spatial distribution of this diversity and (iii) the speed of the epidemic. In particular, if the introduction of virulent genotypes is conditional on a mutation event, the mutant genotype will emerge later than if genetic diversity is present at the onset of the epidemic. This affects the frequency of mutants for all the different values of selection intensity. When selection is strong, the late arrival of the mutant has also a direct impact on the speed of the front and, consequently, on the overall size of the epidemic (compare the radius of the infected population in E and F, see also Figure 3.6). The strength of selection also affects the distribution of genetic diversity. In the absence of selection we recover the patterns described by [119]. The interplay between the spatial spread of the epidemic and the stochasticity occuring at the front generates characteristic quadrants that are either dominated by one genotype or the other. When there is some selection we can recover these quadrants but their shape is altered by competitive interactions (Figure 3.5). At the front line of the epidemic the mutant is a better coloniser and spreads faster. Behind the front, the wild type genotype is more competive and tends to replace the mutant genotype. When selection is strong the mutant only appears at the front and the core of the epidemic is dominated by wild type genotypes.

3.4 Discussion

Improving our ability to control infectious diseases requires a better understanding of both the epidemiology and the evolution of pathogens. Our theoretical understanding of virulence evolution is often based on the assumption that evolution occurs on a much slower time scale than epidemiological dynamics. Yet, epidemiological and evolutionary time scales overlap in many pathogens because large amount of genetic variation fuel the rate of adaptation [132]. In these situations, evolutionary epidemiology theory provides a way to describe accurately the pathogen dynamics during an epidemic and shows how epidemiology can feed-back on evolution [37, 145, 93, 70, 96, 53, 30]. During the early stage of the epidemic more virulent and transmissible strains are favoured because susceptible hosts are abundant. Later on, the density of susceptible hosts is reduced and can reverse the selection on virulence and transmission. Here we extend this theoretical framework to account for the spatial spread during epidemics. We show that more virulent genotypes are favoured at the front line of the epidemic and counterselected behind the front. This heterogeneity of selection is akin to the classical distinction between r and K selection during an invasion [150, 168, 169]. This spatially and temporally variable selection has the ability to maintain diversity. Interestingly, the speed of the whole epidemic (both the wild type and the mutant genotypes) is mainly governed by the presence of the virulent mutant at the front. Hence, even though the presence of the mutant may be limited to a very small range behind the front (in particular when K_m is small) the epidemic may spread much faster when mutation is allowed because the epidemic is pulled by the spread of the virulent mutant at the front. In other words, pathogen evolution feeds back on epidemiological dynamics by speeding up the spread of the pathogen's traveling wave. This result points out a possible flaw in our ability to infer pathogen's growth rate from the speed of the epidemic. If the genotypes at the front are distinct from the ones spreading behind the front, the speed may only help characterize the growth rate of a fraction of the pathogen population. Our analysis is limited to a situation with only two genotypes (the wild type and the mutant). It would be interesting to allow for a continuum of genotypes. We believe that this scenario would yield similar outcomes: we expect that at the front line, genotypes maximizing the Malthusian fitness would be selected, while behind it, genotypes with higher carrying capacity would dominate. Hence, we would retrieve the dichotomy assumed in the present model and observe a continuous phenotypic gradient between these two extremes [164, 5].

Empirical evidence supporting the above theoretical predictions require an intense sampling effort across a moving epidemic. An interesting biological system is the virus dynamics observed in honeybee colonies along a new expansion front [155]. Virus transmission is often tightly linked with the presence of the parasitic mite *Varroa destructor*. In particular the acute bee paralysis virus (ABPV) and the deformed wing virus (DWV) are actively transmitted by *Varroa*. Interestingly, the virulence of ABPV is much higher than the virulence of DWV. In line with our theoretical predictions the ABPV is often found at the edge of the front and is rapidly outcompeted by the DWV [155]. This pattern may be driven by selection for a r-strategy (APBPV) at the fontline and selection for a K-strategy (DWV) behind the front. ABPV and DWV, however, belong to different species complex and mutation does not seem to provide the ability to jump between these different virus forms. This pattern is akin to ecological successions [188] but is not driven by mutation and selection. Further confirmation of the importance of mutation and evolution was obtained with the fungal pathogen *Batrachochytrium dendrobatidis* (*Bd*) in common garden experiments. This pathogenic fungus is known to be the main driver of the recent decline of many amphibian populations around the world [29, 199]. The wave-like spread of this pathogen in Central America has been well monitored [134]. Besides, genetic evidence suggests the ability of mutations to generate a new hypervirulent strain of *Bd* [134, 85, 195]. This biological system has thus all the key elements of our model (spatial spread and mutation). Interestingly, Phillips and Puschendorf [167] discuss the possibility that *Bd* virulence may have increased at the front line of the epidemic. This evidence, however, is indirect because it is based on the rate of decline of the host population after the contact with *Bd* and many other abiotic factors may be involved. It would be particularly interesting to confirm this trend in a common garden experiments. Such an experiment was carried out to monitor the evolution of the nematode lungworm (*Rhabdias marina*), a parasite of the invasive cane toads (*Rhinella marina*) in Australia [135]. Nematodes from the edge of the invasion exhibited very distinct life history traits (larger eggs, larger free-living larvae, larger infective larvae and reduced age at maturity). These results support the general prediction that pathogens may rapidly evolve colonizer syndromes. Whether this evolution leads to higher virulence and faster epidemic spread is unclear in this particular system where the pathogen follows the spread of its host with a lag of several years. What limits the speed is more the availability of the host than the intrinsic epidemic speed. It would be interesting to expand the analysis of our model to a scenario where the speed of the host is lower than the speed of the pathogen. In this case, the pathogen present at the edge of the front experiences a relatively low density of hosts and this may select for lower virulence strategies (see also discussion in [189] where the pathogen may affect the speed of the host invasion).

Experimental evolution may also provide ways to test our predictions. Complex life-history trade offs may emerge in bacteriophages because the instantaneous rate of growth of lytic phages is governed by a limited number of traits (adsorption rate, lysis time, burst size, [52]). Besides, the adsorption rate is also acting on the diffusion rate of the phage [95]. Under these conditions spatial structure is expected to select for lower infectivity and virulence [41, 127, 148, 147]. Several experiments have confirmed that spatial structure can select for less aggressive pathogen strategies in bacteriophages [81, 183, 31]. But those studies never focused on the spatial distribution of the different types of strains across an epidemic. Yin [210], however, realized a very nice experiment with phage T7 where evolution was monitored during the spatial spread of the virus. Unlike other lytic phages, T7 has the ability to form plaques that grow indefintely large on agar plates [209]. Monitoring the growth of the plaque allowed to determine the speed of the epidemic and sampling across the plaque allowed to detect the emergence and the fixation of phage mutants at the edge of the front. Those mutants were characterized with higher fitness in both liquid and spatially structured environments [210] and it is unclear if this particular system matches the underlying assumptions of our model (i.e. $r_m > r_w$ and $K_w > K_m$). But further work using Yin's experimental approach and detailed phenotypic characterisation of the strains across an epidemic could help test some of our theoretical predictions.

The analysis of the stochastic version of our model reveals three effects of finite host population size. First, finite population size has a direct effect on the speed of a monomorphic population. Smaller population sizes reduce the speed because they induce a cutoff in the tail of the distribution at the forefront of the epidemic [51, 192]. Second, the magnitude of this effect depends on the life-history traits of the pathogen: the effect is stronger on the virulent genotype than on the wild type because stochasticity is driven by the population size of each genotype. The lower carrying capacity of the mutant makes it more susceptible to the effect of stochasticity mediated by total host population size N. Hence, the speed of the virulent mutant may become lower than the wild type. Third, stochasticity may result in the extinction of the mutant at the edge of the front. This is related to the effect of the basic reproductive ratio on the probability of emergence [97]. The probability of emergence (i.e. the probability of non-extinction) is driven by the the basic reproductive ratio and thus by K_i. When mutation is allowed, small population sizes may thus prevent the establishment of the virulent mutant at the edge of the front because $K_w > K_m$. This effect may further decrease the speed of the epidemic. These multiple effects may provide a particularly efficient way to slow down an epidemic. Lowering the availability of some hosts by prophylactic intervention is expected to reduce the local transmission rate (and thus both r_i and K_i) but it may also allow these stochastic effects to play in. It is interesting to discuss the effects of stochasticity in the light of recent population genetics theory on gene surfing [118, 119, 163]. Gene surfing is mostly studied in scenarios describing the establishment of neutral or deleterious mutations during an invasion. In our model, selection is not homogeneous in space and time because epidemiology feeds back on the relative fitness of the mutant via the availability of susceptible hosts. This type of selection, when it is strong, can dramatically alter the spatial distribution of genotypes (Figure 3.4). Epidemiological phylodynamics may provide a way to test some of our predictions. For instance Biek et al [34] analysed the spatial spread of rabies virus in North American racoons. Their data was consistent with gene surfing models where different strains occupy different sectors of the spreading disk of the epidemic. More elaborate techniques have also been used to estimate pathogen life history parameters [172]. These new theoretical developments and the availability of more genetic information may provide a way to infer the most likely epidemiological scenario from the examination of spatial distributions of genetic diversity (Figure 3.4).

It is worth pointing out that our model could also be used to better understand coevolution between virulence and antigenic drift occuring in influenza virus in the absence of geographic spatial structure. Influenza evolution is often described as a traveling wave in phenotypic space where the strains at the edge of the front are the ones that are not recognized by the host immune system [110, 38]. In those models the diffusion coefficient in phenotypic space refers to the mutation occuring between strains with different antigens. New strains have access to a higher density of susceptible hosts and this could affect selection acting on other life history traits (transmission and virulence). Our results show that one could expect pathogen virulence to be higher at the edge of this front, and to decrease in older strains because of herd immunity. Yet, to explicitly model the joint evolution of antigenic drift and virulence it is necessary to take into account the genetic linkage between those traits [71].

Evolutionary theory has shown that the adaptation of invasive species may involve a multiplicity of life-history traits. In particular, the diffusion parameter σ is likely to be under strong positive selection at the edge of the front [189]. In our model the diffusion rate is under the control of the host. Other life cycles with free-living stages may be considered, where this trait could be under the control of the pathogen. Further theoretical developments are required to analyse scenarios where multiple other traits may coevolve with virulence and transmission [54, 165, 161]. Besides, it would be particularly relevant to consider the possibility that pathogens spread in a heterogeneous host habitat (e.g. multiple host environments). The impact of various forms of heterogeneity on the spread of invasive species has been studied in monomorphic populations [188]. Allowing mutation would fuel pathogen evolution and could lead to alternative routes of adaptation where pathogens could either specialise on some host or evolve more generalist strategies. In a broader perspective, we believe that a better understanding of the spatial dynamics of pathogens requires detailed studies of the interplay between demography, stochasticity and evolution occuring at the front line of epidemics.

Simulation code

The simulation code was written in C++. It is available online at the address below.
`https://gitlab.com/virulence_evolution_at_the_front_line_of_spreading_epidemics/Virulence_Evolution_at_the_front_line_of_spreading_epidemics_IBM.git`

Competing interests

We have no competing interests.

Author's contribution

SG and GR performed the modeling work, QG conducted the mathematical and numerical analysis. QG and SG wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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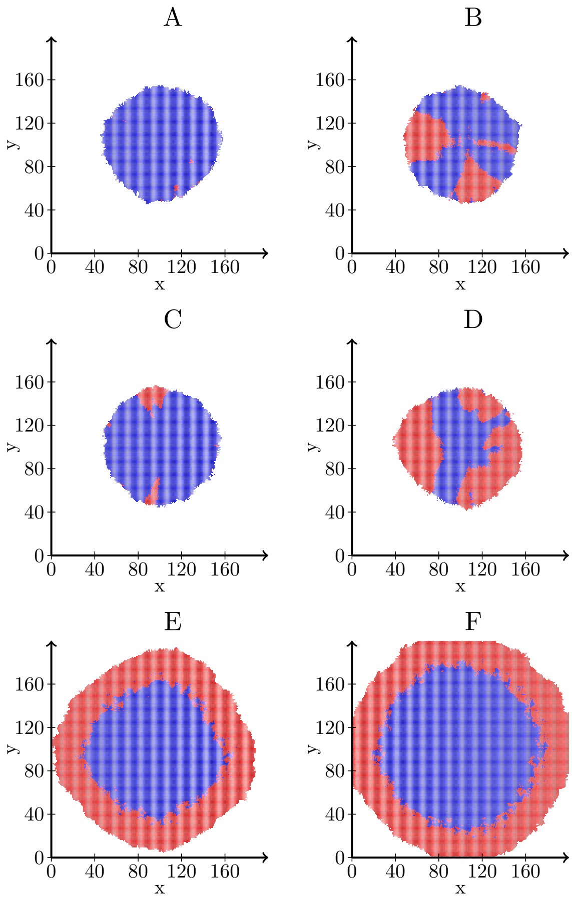

Figure 3.5 – Stochastic simulations of the spread of an epidemic in 2 dimensions (x and y). At the beginning of the simulation the pathogen population starts as a disk of radius 6.3 cells. In A, C and E the simulation starts from an initial condition where only the wild type is present. In B, D and F the simulation starts from a mixed pathogen population where the wild type and the mutant are equally frequent. In the first row (A and B) the wild type and the mutant have the same parameter values (neutral selection scenario). In the second row (C and D) the mutant is slightly more virulent than the wild type (weak selection scenario). In the third row the mutant is very different from the wild type (strong selection scenario). The actual parameters we used can be found in the SI (section 12).

3.5 Supplementary information

3.5.1 The model

The model we describe in the main text can be written as a set of reaction-diffusion equations:

$$\begin{cases} \frac{\partial S}{\partial t} &= \sigma \frac{\partial^2 S}{\partial x^2} - \frac{\beta_w}{N} S I_w - \frac{\beta_m}{N} S I_m + \alpha_w I_w + \alpha_m I_m, \\ \frac{\partial I_w}{\partial t} &= \sigma \frac{\partial^2 I_w}{\partial x^2} + \frac{\beta_w}{N} S I_w - \alpha_w I_w + \mu_m I_m - \mu_w I_w, \\ \frac{\partial I_m}{\partial t} &= \sigma \frac{\partial^2 I_m}{\partial x^2} + \frac{\beta_m}{N} S I_m - \alpha_m I_m + \mu_w I_w - \mu_m I_m. \end{cases} \tag{3.6}$$

We assume that the total density of hosts is initially uniformly distributed in space, with a local population size equal to N, which yields:

$$\begin{cases} \frac{\partial (S+I_w+I_m)}{\partial t} = \sigma \frac{\partial^2 (S+I_w+I_m)}{\partial x^2}, \\ S(t=0) + I_w(t=0) + I_m(t=0) = N. \end{cases} \tag{3.7}$$

The unique solution of (3.7) is the constant solution $(S + I_w + I_m) \equiv N$. Writing $S = N - (I_w + I_m)$, we can then reduce our system to:

$$\begin{cases} \frac{\partial I_w}{\partial t} &= \sigma \frac{\partial^2 I_w}{\partial x^2} + \frac{\beta_w}{N} I_w \left(N - (I_w + I_m)\right) - \alpha_w I_w + \mu_m I_m - \mu_w I_w, \\ \frac{\partial I_m}{\partial t} &= \sigma \frac{\partial^2 I_m}{\partial x^2} + \frac{\beta_m}{N} I_m \left(N - (I_w + I_m)\right) - \alpha_m I_m + \mu_w I_w - \mu_m I_m, \end{cases}$$

or

$$\begin{cases} \frac{\partial I_w}{\partial t} &= \sigma \frac{\partial^2 I_w}{\partial x^2} + (\beta_w - \alpha_w) I_w \left(1 - \frac{I_w + I_m}{N\left(\frac{\beta_w - \alpha_w}{\beta_w}\right)}\right) + \mu_m I_m - \mu_w I_w, \\ \frac{\partial I_m}{\partial t} &= \sigma \frac{\partial^2 I_m}{\partial x^2} + (\beta_m - \alpha_m) \left(1 - \frac{I_w + I_m}{N\left(\frac{\beta_m - \alpha_m}{\beta_m}\right)}\right) + \mu_w I_w - \mu_m I_m. \end{cases}$$

Finally, if for $i \in \{w, m\}$, we introduce the notations

$$r_i = \beta_i - \alpha_i, \quad K_i = N\left(1 - \frac{\alpha_i}{\beta_i}\right), \tag{3.8}$$

then (3.6) becomes

$$\begin{cases} \frac{\partial I_w}{\partial t} &= \sigma \frac{\partial^2 I_w}{\partial x^2} + r_w I_w \left(1 - \frac{I_w + I_m}{K_w}\right) + \mu_m I_m - \mu_w I_w, \\ \frac{\partial I_m}{\partial t} &= \sigma \frac{\partial^2 I_m}{\partial x^2} + r_m I_m \left(1 - \frac{I_w + I_m}{K_m}\right) + \mu_w I_w - \mu_m I_m. \end{cases}$$

3.5.2 Derivation of the speed

Numerical computations (see [114]) and rigorous results for related models (see e.g. [141, 205]) show that the dynamics of a pathogen population initially present in a limited region only is well described by traveling waves solutions. Traveling wave solutions are particular solutions where the pathogens propagate through space at a constant speed. In this section, we detail how the speed of the traveling waves can be derived.

Ahead of the epidemic front, the density of pathogens, that is $(I_w + I_m)$ is very low, and the competition terms $-r_i I_i \frac{I_w+I_m}{K_i}$ (for $i \in \{w, m\}$) can be neglected in (3.1). Ahead of the front, (3.1) can then be reduced to

$$\begin{cases} \frac{\partial I_w}{\partial t} & \approx \sigma \frac{\partial^2 I_w}{\partial x^2} + (r_w - \mu_w) I_w + \mu_m I_m \\ \frac{\partial I_m}{\partial t} & \approx \sigma \frac{\partial^2 I_m}{\partial x^2} + (r_m - \mu_m) I_m + \mu_w I_w. \end{cases} \tag{3.9}$$

We want to consider traveling wave solutions, that is a particular solution (I_w, I_m) that satisfies $(I_w, I_m)(t, x) = (\tilde{I}_w, \tilde{I}_m)(x - ct)$ for a certain unknown speed $c \in \mathbb{R}$. Ahead of the front, $x \mapsto (\tilde{I}_w, \tilde{I}_m)(x)$ (that we denote by $x \mapsto (I_w, I_m)(x)$ for the rest of this section, for the sake of simplicity) must then satisfy:

$$\begin{cases} -cI'_w(x') - \sigma I''_w(x') & \approx (r_w - \mu_w) I_w + \mu_m I_m, \\ -cI'_m(x') - \sigma I''_m(x') & \approx (r_m - \mu_m) I_m + \mu_w I_w. \end{cases} \tag{3.10}$$

The positive solutions of this system write $(I_w, I_m)(x) = e^{-\lambda x}(\bar{I}_w, \bar{I}_m)$ for some λ, $\bar{I}_w$, $\bar{I}_m > 0$. Such functions are solutions of (3.10) if and only if

$$\left(c\lambda - \sigma\lambda^2\right) e^{-\lambda x} \begin{pmatrix} \bar{I}_w \\ \bar{I}_m \end{pmatrix} = e^{-\lambda x} A \begin{pmatrix} \bar{I}_w \\ \bar{I}_m \end{pmatrix},$$

where the matrix A is given by

$$A = \begin{pmatrix} r_w - \mu_w & \mu_m \\ \mu_w & r_m - \mu_m \end{pmatrix}.$$

For each location x, $(c\lambda - \sigma\lambda^2)$ is then an eigenvalue of A, and $(\bar{I}_w, \bar{I}_m)$ an associated eigenvector. We want additionally that $\bar{I}_w$ and $\bar{I}_m$ to be positive. Thanks to the Perron-Frobenius theorem, there exists a unique (up to a multiplication factor) such eigenvector, called principal eigenvector, associated to the largest eigenvalue of A, that we denote by h_+.

We can compute explicitly this principal eigenvalue h_+:

$$\begin{aligned} h_+ \quad = \quad & \frac{1}{2}\left(r_w + r_m - (\mu_w + \mu_m)\right) \\ & + \frac{1}{2}\sqrt{(r_m - r_w)^2 + 2r_w(\mu_m - \mu_w) + 2r_m(\mu_w - \mu_m) + (\mu_w + \mu_m)^2}. \end{aligned} \tag{3.11}$$

(3.10) will then have a solution if and only if there exists $\lambda > 0$ such that $c\lambda - \sigma\lambda^2 = h_+$, that is if $\Delta = c^2 - 4\sigma h_+ \geq 0$. The minimal speed for which a solution of (3.10) exists is then $c_* := 2\sqrt{\sigma h_+}$. In [114], we have shown that there exists indeed a traveling wave of (3.1) for this minimal speed c^*.

To see that the minimal speed c^* is the biologically relevant one, let us denote by $(\tilde{I}_w, \tilde{I}_m)$ the solution of (3.10) that we have just constructed, and $(t,x) \mapsto (I_w, I_m)(t,x)$ a solution of (3.1) initially positive in a limited region only. Then, provided $C > 0$ is chosen large enough, we have

$$\forall x \in \mathbb{R}, \quad I_w(x) \leq \tilde{I}_w(x), \quad I_m(x) \leq \tilde{I}_m(x).$$

One can check that this estimate, combined to the fact that $(\tilde{I}_w, \tilde{I}_m)$ (resp. (I_w, I_m)) is a sub-solution (resp. solution) of (3.9) implies that this ordening is kept through time, that is

$$\forall (t,x) \in \mathbb{R}_+ \times \mathbb{R}, \quad I_w(t,x) \leq \tilde{I}_w(x - c_* t), \quad I_m(t,x) \leq \tilde{I}_m(x - c_* t).$$

This estimate implies that the population propagates at speed at most c_*. Proving that the population does not propagate slower than c^* requires more work (notice however that we have already shown that there exist no traveling waves of (3.1) for speeds lower than c_*).

3.5.3 Position and speed of the front

We present a supplementary figure representing the position of the front as a function of time, in numerical computations of the deterministic model (3.1) (Figure 3.6). We chose our parameters to show the invasion can be described in two phases:

- Initially, the population is dominated by the wild type and the speed of the invasion is then dictated by the intrinsic speed of this population, that is $c \sim 2\sqrt{\sigma r_w}$ (see Remark 3.5.1 in section 3.5.8).
- After some time the mutant pathogens appear by mutation and the mutant population becomes dominant at the edge of the front. After this settling phase, the speed of the invasion is given by c_* (see Section 3.5.2), which is indeed close to the intrinsic speed of the mutant population, that is $c \sim 2\sqrt{\sigma r_m}$ (see Remark 3.5.1 in section 3.5.8).

Note the small acceleration of the front between these two phases due to the modification of the shape of the front, during a short transitory phase.

3.5.4 Approximation for the mutant's area

It is interesting to derive an estimate of the area where mutant pathogens are prevalent in the pathogen populations. Unfortunately, this type of estimate seems out of reach so far with rigorous methods (we refer to [114] for some

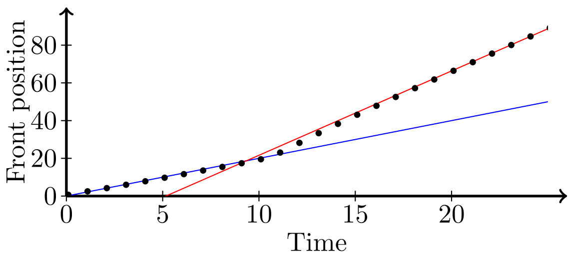

Figure 3.6 – Position of the front with respect to time. The black dots represent the location where the wild type population reaches half its carrying capacity (ie. $w = 1/2$), measured on a numeric computation of Equation (3.1). The initial population that we have considered is composed of only a non-zero population of wild type pathogens located at the origin, while no mutant pathogen are present: $(w, m) = (\delta_0, 0)$ on the box $[0, 500]$. We used the parameters $\sigma = 1$, $r_w = 1$, $r_m = 5$, $K_w = 1$, $K_m = 0.25$, $\mu_w = 10^{-6}$, $\mu_m = 0.01$, and the spatial steps $\Delta t = 0.01, \Delta x = 0.01$. The blue and red lines have a respective constant velocity of $2\sqrt{\sigma r_w}$ and $c^* \sim 2\sqrt{\sigma r_m}$. We have introduced an important asymmetry between μ_w and μ_m to improve the readability of the figure.

rigorous qualitative results on the traveling wave solutions of (3.1)). In this section we will provide a non-rigorous approximation of this area.

We denote by $t \mapsto I_m(t)$ (resp. $t \mapsto I_w(t)$) the population of mutant (resp. wild type) pathogen at a given location. We consider a simplified scenario where some mutant pathogen appears (i.e. $I_m(t) \approx C_0$ for some constant $C_0 > 0$) at a given location at time $t = 0$. If we neglect the spatial and competition effects, the population of mutant pathogens at this location, $I_m(t)$ satisfies

$$I_m(t) = C_0 e^{r_m t},$$

and $I_m(t)$ then reaches its carrying capacity K_m after a time

$$t_0 = \frac{1}{r_m} \log\left(\frac{K_m}{C_0}\right) \sim \frac{1}{r_m} \log\left(K_m\right). \tag{3.12}$$

Once these mutant pathogens are present, we assume that their population remains of size K_m as long as they are more numerous than the wild type pathogens. Some wild type pathogens appear inside the established mutant population through mutations, and begin to reproduce on their own. If we neglect the wild types produced by mutation before time t_0 (this can be done if μ_m is small), the impact of the spatial structure of the problem and the effects of competition, the size of the population of the wild type pathogens satisfies, for $t \geq t_0$,

$$\begin{cases} I_w'(t) & \approx r_w I_w(t)\left(1-\frac{K_m}{K_w}\right)+\mu_m K_m, \\ I_w(t_0) & \approx 0, \end{cases}$$

The solution of this ordinary differential equation is then:

$$\begin{aligned} I_w(t) &\approx \frac{\mu_m K_m}{r_w\left(1-\frac{K_m}{K_w}\right)}\left(e^{r_w\left(1-\frac{K_m}{K_w}\right)(t-t_0)}-1\right) \\ &\approx \frac{\mu_m K_m}{r_w\left(1-\frac{K_m}{K_w}\right)} e^{r_w\left(1-\frac{K_m}{K_w}\right)(t-t_0)}, \end{aligned}$$

where this last approximation holds when μ_m is small. From this expression, we deduce that the wild type becomes dominant (that is $I_w \geq K_m$) at a time

$$\begin{aligned} t_1 &\approx t_0 + \frac{1}{r_w\left(1-\frac{K_m}{K_w}\right)} \log\left(\frac{r_w\left(1-\frac{K_m}{K_w}\right)}{\mu_m}\right) \\ &\sim t_0 + \frac{1}{r_w\left(1-\frac{K_m}{K_w}\right)} \log\left(\frac{1}{\mu_m}\right), \end{aligned}$$

where we have used the fact that μ_m is small. This estimate combined to (3.12) provides an estimate of t_1, the period of time during which the mutant population is significant and dominant. Obtaining an estimate on the area where the mutant population is significant and dominant is then easy, since the pathogen are invading space at speed c_* (see Section 3.5.2):

$$a_m = c_*(t_0+t_1) \approx \frac{2\sqrt{\sigma}}{\sqrt{r_m}} \log K_m + \frac{2\sqrt{\sigma r_m}}{r_w\left(1-\frac{K_m}{K_w}\right)} \log\left(\frac{1}{\mu_m}\right).$$

3.5.5 Mutation-selection equilibrium behind the front

Behind the front of the epidemic, the population reaches a mutation-selection equilibrium (see [114]), and the the spatial dynamics of the epidemic can be neglected. We will show in this section that in a homogeneous setting, the population converge to a unique stable equilibrium. The population behind the edge of the invasion will thus correspond to this equilibrium.

To improve the readability, we write $I := I_m + I_w$ and $p := \frac{I_m}{I}$. We can formulate the dynamics of the populations in terms of p and I:

$$\frac{d}{dt}p = \frac{\frac{d}{dt}I_m I - I_m \frac{d}{dt}I}{I^2} = \frac{\frac{d}{dt}I_m}{I} - p\frac{\frac{d}{dt}I}{I}, \tag{3.13}$$

$$\begin{aligned}\frac{d}{dt}I &= r_m\left(1-\frac{I}{K_m}\right)I_m + r_w\left(1-\frac{I}{K_w}\right)I_w \\ &= I\left(r_m\left(1-\frac{I}{K_m}\right)p + r_w\left(1-\frac{I}{K_w}\right)(1-p)\right), \end{aligned} \tag{3.14}$$

and finally:

$$\frac{d}{dt}I_m = r_m\left(1-\frac{I}{K_m}\right)pI + \mu_w(1-p)I - \mu_m pI. \tag{3.15}$$

Combining Equations (3.13), (3.14) and (3.15), we get:

$$\frac{d}{dt}p = \left[I\left(\frac{r_w}{K_w}-\frac{r_m}{K_m}\right) + r_m - r_w\right]p(1-p) + \mu_w(1-p) - \mu_m p.$$

One can define the selection coefficient against the mutant as

$$s = r_w - r_m - I\left(\frac{r_w}{K_w}-\frac{r_m}{K_m}\right).$$

In order to simplify the analysis, we make the reasonable assumptions that i) the mutation rates of the mutant and the wild type are small and ii) that the total equilibrium population of infected is close to $I = K_w$. Indeed, because the mutation rates are low, the frequency of the mutant is also low at equilibrium. Following these assumptions, we can now compute the equilibrium frequency of the mutant using:

$$\dot{p} \sim -sp(1-p) + \mu_w(1-p) = 0,$$

which yields:

$$p_{eq} \sim \frac{\mu_w}{s}.$$

3.5.6 Two complementary scenarios

The goal of this section is to give additional details about the two alternative scenarios discussed in the main text.

With no host reproduction

First we examine a situation where the host is not allowed to reproduce. In other words, the host population size is not fixed but drops when the infection spreads. In this case the epidemic cannot reach an endemic state because the density of infected hosts also drops behind the front of the epidemic. This yields the following model :

$$\begin{cases} \frac{\partial S}{\partial t} &= \sigma\frac{\partial^2 S}{\partial x^2} - \beta_w S I_w - \beta_m S I_m \\ \frac{\partial I_w}{\partial t} &= \sigma\frac{\partial^2 I_m}{\partial x^2} + \beta_w S I_w - \alpha_w I_w + \mu_m I_m - \mu_w I_w \\ \frac{\partial I_m}{\partial t} &= \sigma\frac{\partial^2 I_w}{\partial x^2} + \beta_m S I_m - \alpha_m I_m + \mu_w I_w - \mu_m I_m \end{cases} \tag{3.16}$$

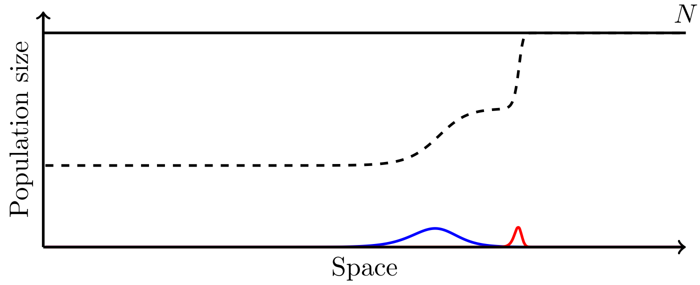

Figure 3.7 – Shape of the stationary solution for a SI scenario with host demography. Hosts are not allowed to reproduce and host death is only induced by the infection. The number of susceptible hosts is also shown (black dashed curve). For clarity, we multiplied the population size of the mutant and wild type strains by 5. Parameters : $\beta_w = 10.0$, $\alpha_w = 5.0$, $r_w = 5.0$, $\mu_w = 0.01$, $R_{0,w} = 2.0$, $\beta_m = 50.0$, $\alpha_m = 40.0$, $r_m = 10.0$, $\mu_m = 0.01$, $R_{0,m} = 1.25$, $\sigma = 1.0$.

This scenario may be relevant in situations where a virulent pathogen spreads rapidly in a host population. This model may thus be more relevant to describe the epidemiology of many infectious diseases of plants or bacterial microbes. In particular, it may be used to model the spread of lytic bacetriophages in a bacterial lawn of bacteria on agar plates. When the bacteria have exhausted the resource they stop reproducing but some lytic phages manage to replicate and diffuse spatially [209, 210]. Figure 3.7 shows the density of both pathogen strains together with the density of susceptible hosts to better see the impact of the epidemic on host demography. We recover the qualitative pattern described in our first model: the virulent mutant is present at the edge of the front, but it is outcompeted behind the front.

With host recovery and immunity

Second, we study a classical SIR model with constant host population size, in which hosts acquire immunity at rate γ and lose it at rate θ. The epidemic can reach an endemic equilibrium behind the front but the prevalence at this endemic equilibrium is much lower than in the SI model because of herd immunity. This yields the following model :

$$\begin{cases} \frac{\partial S}{\partial t} &= \sigma \frac{\partial^2 S}{\partial x^2} - \beta_w S I_w - \beta_m S I_m + \theta R \\ \frac{\partial I_w}{\partial t} &= \sigma \frac{\partial^2 I_w}{\partial x^2} + \beta_w S I_w - \gamma_w I_w + \mu_m I_m - \mu_w I_w \\ \frac{\partial I_m}{\partial t} &= \sigma \frac{\partial^2 I_m}{\partial x^2} + \beta_m S I_m - \gamma_m I_m + \mu_w I_w - \mu_m I_m \\ \frac{\partial R}{\partial t} &= \sigma \frac{\partial^2 R}{\partial x^2} + \gamma_w I_w + \gamma_m I_m - \theta R. \end{cases} \tag{3.17}$$

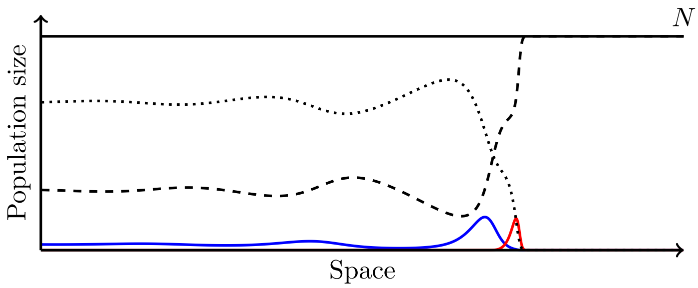

Figure 3.8 – Shape of the stationary solution for a SIR scenario. We use an SIR model in which infected hosts I_w (resp. I_m) acquire immunity at rate γ_w (resp. γ_m) and any recovered host loses immunity at rate θ. The number of recovered hosts is also shown (black dotted curve). Parameters : $\beta_w = 2.0$, $\alpha_w = 0.05$, $\gamma_w = 0.5$, $r_w = 1.45$, $\mu_w = 0.01$, $R_{0,w} = 3.64$, $\beta_m = 10.0$, $\alpha_m = 6.0$, $\gamma_m = 1.0$, $r_m = 3.0$, $\mu_m = 0.01$, $R_{0,m} = 1.43$, $\theta = 0.02$, $\sigma = 1.0$.

This pathogen's life cyle corresponds to situations where clearance is a likely outcome of the infection. This model may be relevant to describe the epidemiology of many infectious diseases of animals. Figure 3.8 shows the density of both pathogen strains together with the density of recovered hosts to better see the impact of the epidemic on host demography. Note that the transient dynamics toward the endemic equilibrium behind the front may be characterised by damped oscillations. Again, we recover the same qualitative pattern as described in our first model: the virulent mutant is present at the edge of the front, but it is outcompeted behind the front.

3.5.7 From an Individual-Based Model to the deterministic model

An Individual-Based Model

We consider a population of individuals on a discrete space $h\mathbb{Z}$, with $h > 0$. We consider three types of individuals: susceptible (S), infected by a wild type pathogen (I_w) and infected by a mutant pathogen (I_m). We denote $\mathcal{S} = \{S, I_w, I_m\}$ the set of all possible states. At any time $t > 0$, we represent the population by a finite counting measure

$$\nu_t = \sum_{i=0}^{P(t)-1} \delta_{x_t^i} \tag{3.18}$$

where $P(t)$ is the total number of individuals at time t and $x_t^0, \ldots, x_t^{P(t)-1} \in h\mathbb{Z} \times \mathcal{S}$ is an enumeration of the individuals at time t. We assume a constant population size at each spatial position, which can be expressed by the constraint:

$$\forall i \in h\mathbb{Z}, \nu_t(\{i\} \times \mathcal{S}) = N \tag{3.19}$$

The dynamics of the population is as follows:

- Individuals of type S die and reproduce, but since a dead individual is immediately replaced by an other one to keep a constant population, these events do not affect population dynamics.
- For any couple of individuals containing an individual of type I_w (resp. I_m) and the other one of type S, from the same location $i \in h\mathbb{Z}$, the susceptible one is infected and becomes of type I_w (resp. I_m) with a rate β_w^0 (resp. β_m^0). In other words, the time it takes for this infection to occur follows an exponential law with parameter β_w^0 (resp. β_m^0).

  This process then models a well-mixed population at each location $i \in h\mathbb{Z}$. There are no infection events between individuals in different locations.
- The rate at which a wild type (resp. mutant) infection mutates into a mutant (resp. wild type) is μ_w (resp. μ_m). If such a mutation occurs, the wild type (resp. the mutant) is replaced by a mutant (resp. a wild type).
- An individual infected by the wild type (resp. mutant) pathogen dies with a rate α_w (resp. α_m). We assume that any dead individual is immediately replaced by a healthy one, keeping the population constant.
- A couple of individuals from neighbouring sites exchange their location with rate λ. This last process models random dispersion while keeping the population size constant at each location.

A formal way of describing the underlying Markov process $(\nu_t)_{t\geq 0}$ is through its infinitesimal generator (see e.g. [82]), which here is:

$$\begin{aligned}
L\Phi(\nu) = &\sum_{i\in h\mathbb{Z}} \beta_w^0(\delta_{i,I_w} * \nu)(\delta_{i,S} * \nu)(\Phi(\nu + \delta_{i,I_w} - \delta_{i,S}) - \Phi(\nu))\\
&+ \sum_{i\in h\mathbb{Z}} \beta_m^0(\delta_{i,I_m} * \nu)(\delta_{i,S} * \nu)(\Phi(\nu + \delta_{i,I_m} - \delta_{i,S}) - \Phi(\nu))\\
&+ \sum_{i\in h\mathbb{Z}} \mu_w(\delta_{i,I_w} * \nu)(\Phi(\nu + \delta_{i,I_m} - \delta_{i,I_w}) - \Phi(\nu))\\
&+ \sum_{i\in h\mathbb{Z}} \mu_m(\delta_{i,I_m} * \nu)(\Phi(\nu + \delta_{i,I_w} - \delta_{i,I_m}) - \Phi(\nu))\\
&+ \sum_{i\in h\mathbb{Z}} \alpha_w(\delta_{i,I_w} * \nu)(\Phi(\nu - \delta_{i,I_w} + \delta_{i,S}) - \Phi(\nu))\\
&+ \sum_{i\in h\mathbb{Z}} \alpha_m(\delta_{i,I_m} * \nu)(\Phi(\nu - \delta_{i,I_m} + \delta_{i,S}) - \Phi(\nu))
\end{aligned}$$

$$+ \sum_{(i,j,k)\in h\mathbb{Z}\times\mathcal{S}\times\mathcal{S}} \big(\lambda(\delta_{i,j} * \nu)(\delta_{i+h,k} * \nu)(\Phi(\nu + \delta_{i,k} - \delta_{i+h,k} + \delta_{i+h,j} - \delta_{i,j}) - \Phi(\nu))\big), \tag{3.20}$$

where Φ is a bounded test function.

Derivation of the PDE system

When the population size per cell N is very large, the dynamics of the population presented in Section 3.5.7 is well described by the deterministic model (3.6). In this section, we will explain with non-rigorous arguments how to derive (3.6) from the individual-based model introduced in the last section.

For $i \in h\mathbb{Z}$, let

$$s(i) = \frac{\nu(i, S)}{N}, \quad w(i) = \frac{\nu(i, I_w)}{N}, \quad m(i) = \frac{\nu(i, I_m)}{N}.$$

Thanks to an argument based on the law of large numbers, it is possible to show that for $N > 0$ large, $(i,t) \mapsto (s,w,m)(t,i)$ will concentrate around the solution of the the following system of ordinary differential equations (see e.g. [35] for similar asymptotic arguments):

$$\begin{cases} \partial_t s(i) &= \alpha_w w(i) + \alpha_m m(i) - N\beta_w^0 w(i)s(i) - N\beta_m^0 m(i)s(i) \\ &\quad +N\lambda((s(i+h) + s(i-h))(w(i) + m(i)) \\ &\quad -s(i)(w(i+h) + w(i-h) + m(i+h) + m(i-h))), \\ \partial_t w(i) &= N\beta_w^0 w(i)s(i) - \alpha_w w(i) + \mu_m m(i) - \mu_w w(i) \\ &\quad +N\lambda((w(i+h) + w(i-h))(s(i) + m(i)) \\ &\quad -w(i)(s(i+h) + s(i-h) + m(i+h) + m(i-h))), \\ \partial_t m(i) &= N\beta_m^0 m(i)s(i) - \alpha_m m(i) + \mu_w w(i) - \mu_m m(i) \\ &\quad +N\lambda((m(i+h) + m(i-h))(s(i) + w(i)) \\ &\quad -m(i)(s(i+h) + s(i-h) + w(i+h) + w(i-h))). \end{cases} \tag{3.21}$$

In order to let $N \to +\infty$, we need to allow β_w, β_m and λ to shrink with N. We thus need to interpret β_w^0, β_m^0 as functions of N: $\beta_i^0 = \beta_i^0(N)$. As we will see later, it will be necessary to understand λ as a function of h as well as N: $\lambda = \lambda(N,h)$. We thus assume

$$\beta_w^0(N) = \frac{\beta_w}{N},$$
$$\beta_m^0(N) = \frac{\beta_m}{N},$$
$$\lambda(N,h) = \frac{\sigma}{Nh^2},$$

β_m, β_w and σ being the life-history constants used to describe the life-history of the pathogen in our model. Then,

$$\begin{cases} \partial_t w(i) &= \beta_w w(i)(1 - w(i) - m(i)) - \alpha_w w(i) + \mu_m m(i) - \mu_w w(i) \\ & \quad + \frac{\sigma}{h^2}(w(i+h) + w(i-h) - 2w(i)), \\ \partial_t m(i) &= \beta_m m(i)(1 - w(i) - m(i)) - \alpha_m m(i) + \mu_w w(i) - \mu_m m(i) \\ & \quad + \frac{\sigma}{h^2}(m(i+h) + m(i-h) - 2m(i)). \end{cases}$$

Formally,

$$\frac{w(i+h) + w(i-h) - 2w(i)}{h^2} \underset{h \to 0}{\sim} \partial_{xx} w(i).$$

The discrete solution $(t, i) \mapsto (w, m)(t, i)$ should then converge to the solution $(t, x) \mapsto (w, m)(t, x)$ of

$$\begin{cases} \partial_t w(t,x) &= \beta_w w(t,x)(1 - w(t,x) - m(t,x)) - \alpha_w w(t,x), \\ & \quad +\mu_m m(t,x) - \mu_w w(t,x) + \sigma \partial_{xx} w(t,x) \\ \partial_t m(t,x) &= \beta_m m(t,x)(1 - w(t,x) - m(t,x)) - \alpha_m m(t,x). \\ & \quad +\mu_w w(t,x) - \mu_m m(t,x) + \sigma \partial_{xx} m(t,x) \end{cases}$$

Here also, it should be possible to derive this result rigorously. The convergence is indeed similar to the convergence of solutions of (Euler-explicit) finite difference schemes to the solution of original parabolic equation. We rewrite this system to obtain:

$$\begin{cases} \partial_t w(t,x) - \sigma \partial_{xx} w(t,x) &= (\beta_w - \alpha_w) w(t,x) \left(1 - \frac{w(t,x)+m(t,x)}{1 - \frac{\alpha_w}{\beta_w}}\right) \\ & \quad +\mu_m m(t,x) - \mu_w w(t,x), \\ \partial_t m(t,x) - \sigma \partial_{xx} m(t,x) &= (\beta_m - \alpha_m) m(t,x) \left(1 - \frac{w(t,x)+m(t,x)}{1 - \frac{\alpha_m}{\beta_m}}\right) \\ & \quad +\mu_w w(t,x) - \mu_m m(t,x), \end{cases} \tag{3.22}$$

that is

$$\begin{cases} \partial_t w(t,x) - \sigma \partial_{xx} w(t,x) &= (\beta_w - \alpha_w) w(t,x) \left(1 - \frac{w(t,x)+m(t,x)}{\kappa_w}\right) \\ & \quad +\mu_m m(t,x) - \mu_w w(t,x), \\ \partial_t m(t,x) - \sigma \partial_{xx} m(t,x) &= (\beta_m - \alpha_m) m(t,x) \left(1 - \frac{w(t,x)+m(t,x)}{\kappa_m}\right) \\ & \quad +\mu_w w(t,x) - \mu_m m(t,x), \end{cases} \tag{3.23}$$

where

$$r_i = \beta_i - \alpha_i, \quad \kappa_i = 1 - \frac{\alpha_i}{\beta_i}.$$

We have thus retrieved the model we use in the main text, as well as the links between the different parameters we used. Indeed, with $I_w = Nw$, $I_m = Nm$ and

$$K_i = \kappa_i N = N\left(1 - \frac{\alpha_i}{\beta_i}\right) \text{ for } i \in \{m, w\},$$

we recover the system (3.1) derived in Section 3.5.1

3.5.8 Speed of stochastic invasions

Following Brunet and Derrida [51] we present a derivation of the speed of the invasion when the pathogen population is finite. For a rigorous proof, we invite the reader to refer to [76, 16] and [157] for the consistency of the approximation with the microscopic models.

Speed of the traveling waves for the Fisher-KPP model

We consider here the simpler case of a single pathogen strain invading a population of hosts. The propagation of the pathogen can then be described by the celebrated Fisher-KPP model (see [89, 141]):

$$\partial_t n(t,x) - \partial_{xx} n(t,x) = (1 - n(t,x))\, n(t,x). \tag{3.24}$$

To investigate the propagation speed of the population, we consider traveling wave solutions, that is solutions of (3.24) of the form $n(t,x) = Q(x - ct)$ (for some $c \in \mathbb{R}$), that satisfies

$$\begin{cases} -c\partial_x Q(x) - \partial_{xx} Q(x) = (1 - Q(x))\, Q(x), \\ Q > 0, \, \lim_{x\to-\infty} Q(x) = 1, \, \lim_{x\to+\infty} Q(x) = 0. \end{cases}$$

For large x, $Q(x)$ is small, and the non-linear term in (3.24) can be neglected, so that up to a translation, $Q(x)$ should be equivalent to $P(x)$ for large x, where P satify

$$\begin{cases} -c\partial_x P(x) - \partial_{xx} P(x) = P(x), \\ P > 0, \, \lim_{x\to+\infty} P(x) = 0. \end{cases} \tag{3.25}$$

It can be shown that the speed of the traveling waves of (3.24) is given by its tip (such fronts are often called "pulled fronts": they are driven by the growth of individuals ahead of the front itself). We can then focus on the properties of $P(x)$ for $1 \ll x$, which is equivalent to the properties of $Q(x)$ for $1 \ll x$.

We notice now that the solutions of the linear ordinary differential equation (3.25) can be written explicitly:

$$P(x) = Ae^{-\gamma x} + Be^{-\bar{\gamma} x}, \quad x \in \mathbb{R}, \tag{3.26}$$

where A, $B \in \mathbb{R}$, and γ, $\bar{\gamma}$ are roots of

$$\gamma^2 - c\gamma + 1 = 0, \tag{3.27}$$

and, since we require that $P > 0$, γ, $\bar{\gamma}$ must be real numbers, γ, $\bar{\gamma} \in \mathbb{R}$. Another formulation of (3.27) is the following:

$$c = c(\gamma) := \gamma + \frac{1}{\gamma}. \tag{3.28}$$

Mathematical analysis [141] and numerical computations [89] show that the biologically relevant speed for (3.24), is the minimal speed such that non-negative solutions P of (3.26) exist, that is $c^* := \min_{\gamma\geq 0} c(\gamma) = 2$. The corresponding coefficients in (3.26) are then $\gamma^* = \bar{\gamma}^* = 1$.

Remark 3.5.1. The Fisher-KPP equation (3.24) can be generalized to

$$\partial_t \tilde{n}(t,x) - \sigma\partial_{xx}\tilde{n}(t,x) = r\left(1 - \frac{\tilde{n}(t,x)}{\kappa}\right)\tilde{n}(t,x). \tag{3.29}$$

where $\sigma > 0$ characterize the dispersion of the population, and $r > 0$ its growth rate. This equation is equivalent to (3.24) thanks to the change of variable $\tilde{n}(t,x) = \kappa\, n\left(rt, x\sqrt{\frac{r}{\sigma}}\right)$, so that we can deduce from our arguments above that the minimal speed traveling waves of (3.29) have a speed of $2\sqrt{r\sigma}$, and a profile equivalent to $P(x) = e^{-\sqrt{\frac{r}{\sigma}}x}$ for $1 \ll x$.

Case of a finite population size

If the host population size M (number of host by unit of space) is large, then the model (3.24) is consistent with individual-based models (if we consider that $n(t,x)$ is the proportion of infected hosts at time t and location x), as soon as $1/M \leq n(t,x) \leq 1 - 1/M$, thanks to an argument similar to the one presented in Section 3.5.7. In the case of epidemic fronts however, this property is not satisfied everywhere, and numerical simulations show that the traveling waves of (3.24) overestimate the speed corresponding individual-based models.

In the previous section, we have seen that the speed of traveling waves of (3.24) is determined by the properties of the solutions $x \mapsto P(x)$ of (3.25) for $1 \ll x$. This property still holds here, but only for x satisfying $1 \ll x \leq x^*(M)$, where $x^*(M) := \log M$ is such that $P(x^*(M)) \approx \frac{1}{M}$. For $x^*(M) < x$ on the contrary, since $P(x) < \frac{1}{M}$, there shouldn't be any pathogen present, and thus $P(x) \equiv 0$. In this section, we will discuss how we can connect a solution of (3.25) for $1 \ll x \leq x^*(M)$ to the solution $P(x) \equiv 0$ for $x^*(M) \leq x$. Note finally that $x^*(M) \to \infty$ as $M \to \infty$, so that the set where $1 \ll x \leq x^*(M)$ is actually large (when M is large).

Solutions of (3.25) **for** $1 \ll x \leq x^*(M)$**:** Here, contrary to Section 3.5.8, we require $x \mapsto P(x)$ to be positive for $1 \ll x \leq x^*(M)$ only. We can then consider solutions of the form (3.26) with $\gamma, \bar{\gamma}$ complex numbers.

Since $x \mapsto P(x)$ is real-valued, γ and $\bar{\gamma}$ are complex conjugates:

$$\gamma = \gamma_R + i\gamma_I, \quad \bar{\gamma} = \gamma_R - i\gamma_I,$$

for some γ_R, $\gamma_I \in \mathbb{R}$, and (3.26) becomes

$$P(x) = Ae^{-\gamma_R x} \sin(\gamma_I x).$$

Since we consider a large (although finite) population of hosts $M > 0$, we should be close to the infinite host population considered in Section 3.5.8, and thus $(\gamma, \bar{\gamma})$ will be close to (γ^*, γ^*), i.e.

$$\gamma_R \approx \gamma^* = 1, \quad \gamma_I \approx 0.$$

Note finally that to get that $P(x) > 0$ for $1 \ll x \leq x^*(M)$, we simply need that

$$\gamma_I x^*(M) \lesssim \pi. \tag{3.30}$$

Connection with $P(x) \equiv 0$ **for** $x^*(M) \ll x$**:** To be able to connect the solution constructed above for $1 \ll x \leq x^*(M)$ to $P(x) \equiv 0$ for $x^*(M) \leq x$, we need to have $P(x) = 0$ for some $x \approx x^*(M)$, i.e. $\gamma_I x^*(M) \approx \pi$ (Note that this implies in particular that (3.30) is satisfied), or $\gamma_I \approx \frac{\pi}{x^*(M)} \approx \frac{\pi}{\log M}$. To sum up our approximations, we have estimated that

$$\gamma = \gamma_R + i\gamma_I \approx 1 + i\frac{\pi}{\log M}. \tag{3.31}$$

Estimate on the speed c**:** We can now use this result to estimate the speed c of the front, thanks to (3.28):

$$c \sim (\gamma_R + i\gamma_I) + \frac{1}{\gamma_R + i\gamma_I} = \gamma_R\left(1 + \frac{1}{\gamma_R^2 + \gamma_I^2}\right) + i\gamma_I\left(1 - \frac{1}{\gamma_R^2 + \gamma_I^2}\right).$$

Since c is a real number, its imaginary part is indeed 0, and we can estimate c further thanks to a Taylor expansion and (3.31):

$$c \sim \gamma_R\left(1 + 1 - (\gamma_R^2 + \gamma_I^2 - 1)\right) \sim 2 - \frac{\pi^2}{\log^2 M}. \tag{3.32}$$

Remark 3.5.2. As we have seen in Remark 3.5.1, The Fisher-KPP model (3.24) can be easily generalized to the model (3.29), with σ, $r > 0$. A similar generalization (thanks to a rescaling) can be done in the individual-based model consider in the present section. Each individual then contributing to the density $\tilde{n}(t, x)$ with a weight $\frac{1}{M}$. The estimate (3.32) presented above then becomes

$$c \sim 2\sqrt{r\sigma} - \sqrt{r\sigma}\frac{\pi^2}{\log^2(\kappa M)}. \tag{3.33}$$

Application of the Brunet-Derrida estimate to the wild type and mutant populations

In our study, we are interested in two species of pathogens, with different characteristics. Following the notations of Section 3.5.7, let $w = w(t, x)$ denote the density of the wild type population, and $m = m(t, x)$ the density of mutant population. If we forget the mutations and assume that only one of those species is present (that is either $\mu_w = 0$ and $m \equiv 0$, or $\mu_m = 0$ and $w \equiv 0$, in (3.23)), then we can model those populations by the following Fishet-KPP equations:

$$\partial_t w - \sigma \partial_{xx} w = r_w w \left(1 - \frac{w}{\kappa_w}\right),$$

$$\partial_t m - \sigma \partial_{xx} m = r_m m \left(1 - \frac{m}{\kappa_m}\right),$$

with $\kappa_i = 1 - \frac{\alpha_i}{\beta_i}$. Still following Section 3.5.7, the number of hosts by unit of space is $\frac{N}{h}$, so that each individual is contributing to the density $w(t, x)$ (resp. $m(t, x)$) with a weight $\frac{h}{N}$.

Thanks to (3.33), the propagation speed c_w (resp. c_m) of the wild type pathogen alone (resp. of the mutant type alone) is then given by:

$$c_w^{stoch} \sim 2\sqrt{r_w \sigma} - \sqrt{r_w \sigma} \frac{\pi^2}{\log^2\left(\frac{\kappa_w N}{h}\right)} = 2\sqrt{r_w \sigma} - \sqrt{r_w \sigma} \frac{\pi^2}{\log^2\left(\frac{K_w}{h}\right)},$$
$$c_m^{stoch} \sim 2\sqrt{r_m \sigma} - \sqrt{r_m \sigma} \frac{\pi^2}{\log^2\left(\frac{\kappa_m N}{h}\right)} = 2\sqrt{r_m \sigma} - \sqrt{r_m \sigma} \frac{\pi^2}{\log^2\left(\frac{K_m}{h}\right)}.$$

3.5.9 Behaviour of the stochastic front

We present an interesting dynamics that appeared through our stochastic simulations. To understand better the behaviour of the stochastic front in the intermediate population size (see main text, Figure 3.4), we plotted the instantaneous speed of the front with respect to time and drew the composition of the first cells at the edge of the front as the background color (blue if the wild type is prevalent, red if the mutant is prevalent). The result is shown in Figure 3.9.

This reveals the existence of a mixed dynamics in which the mutant has the ability to invade the front but is stochastically lost due to its small population size. We interpret this pattern as the result of two competing exponential clocks : the one that rules the mutant's invasion (mutation event occuring near the front) and the one that rules its extinction (stochastic extinction of a finite population, since the population of the mutant is limited by its range; see main text).

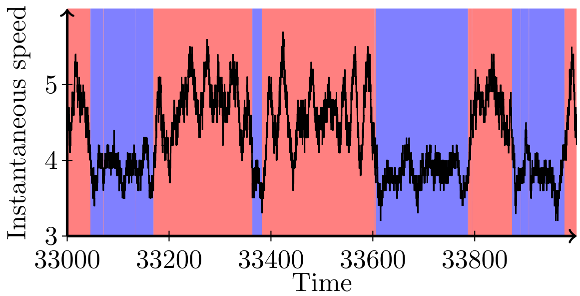

Figure 3.9 – Instantaneous speed of the front of the epidemic across time. The underlying color indicates which pathogen genotype is present at the edge of the front: the wild type (blue) or the mutant (red). This corresponds to a single run of a stochastic simulation of the epidemic spread. Default parameter values: $\beta_w = 5$, $\alpha_w = 1$, $r_w = 4.0$, $R_{0,w} = 5.0$, $\beta_m = 50$, $\alpha_m = 40$, $r_m = 10.0$, $R_{0,m} = 1.25$, $\mu_w = \mu_m = 0.01$, $N = 550$, $\sigma = 1$, $h = 1$. The criterion we used to determine which genotype dominates at the edge is based on their relative abundance in the first three occupied cells. The speed is the shifting speed averaged in a small period of time (5 units). Notice that since the simulations are done in continuous time, there is no discretization step. The unit of time is thus arbitrary, but common to all the simulations: it corresponds to the average life-time of a wild type infection (i.e. $\alpha_w = 1$ in all our simulations).

3.5.10 Link between pathogen life-history traits and demographic parameters

In the paper, we typically use two different sets of parameters:

- the *pathogen life-history traits* β (transmission rate) and α (virulence)
- the *pathogen demographic parameters* r (growth rate) and K (carrying capacity).

We have already shown (see (3.8)) how to obtain demographic parameters from the life-history traits:

$$r = \beta - \alpha, \quad K = N\left(1 - \frac{\alpha}{\beta}\right),$$

but we can also reverse the operation:

$$\begin{cases} r = \frac{\beta}{N} K, \\ K = N\left(1 - \frac{\alpha}{\beta}\right), \end{cases}$$

$$\begin{cases} \beta = \frac{rN}{K}, \\ K = N - \frac{K}{r}\alpha, \end{cases}$$

which yields:

$$\beta = \frac{rN}{K}, \quad \alpha = r\left(\frac{N}{K} - 1\right).$$

3.5.11 Dimensional analysis

In our study we use only three underlying dimensions that we denote P (population), T (time) and D (distance). Table 3.1 is a summary of the different quantities we used and their respective dimensions.

Quantity	Dimension
α_i	T^{-1}
β_i	T^{-1}
β_i^0	$P^{-1}T^{-1}$
h	D
I, I_i	P
K_i	P
λ	$P^{-1}T^{-1}$
μ_i	T^{-1}
N	P
r_i	T^{-1}
σ	D^2T^{-1}

Table 3.1 – Quantities vs. dimensions ($i \in \{w, m\}$)

3.5.12 Main text figures

Here is the detail of the parameters we used to produce the main text figures and some additional information :

- Figure 3.2 : $r_w = 1$, $K_w = 1$, $\beta_w = 2$, $\alpha_w = 1$, $R_{0,w} = 2$, $\mu_m = \mu_w = 0.001$, $r_m = 2$, $K_m = 0.5$, $\beta_m = 8$, $\alpha_m = 6$, $R_{0,m} = 1.3$, $N = 2$, $\sigma = 1$.

- Figure 3.3 : We used a parabolic implicit finite-difference scheme on the interval $[0, 500]$ with a spatial step of $h = 0.01$, a time step of $dt = 0.01$ and an initial condition where the wild type is a dirac mass at $x = 0$ and the mutant is absent. Default parameter values: $\sigma = 1$, $r_w = 1$, $K_w = 1$, $r_m = 2$, $K_m = 0.25$, $\mu_w = 0.001$, $\mu_m = 0.001$. With $N = 2$ and those parameters we have then $\beta_w = 2$, $\alpha_w = 1$, $R_{0,w} = 2$, $\beta_m = 16$, $\alpha_m = 14$, $R_{0,m} = 1.14$.

- Figure 3.4 : Default parameter values: $\sigma = 1$, $\beta_w = 5$, $\alpha_w = 1$, $r_w = 4$, $R_{0,w} = 5$, $\beta_m = 50$, $\alpha_m = 40$, $r_m = 10$, $R_{0,m} = 1.25$, $\mu_w = \mu_m = 0.01$, $h = 1$.

- Figure 3.5 : Default parameter values: $N = 100$, $\sigma = 1$, $\mu_w = \mu_m = 0.005$. As in Figure 3.9, the simulations are carried out in continuous time: there is no other discretization than the floating-point representation of real numbers. For each scenario the rest of the parameters have different values :

  - neutral selection scenario : $\beta_w = \beta_m = 5$, $\alpha_w = \alpha_m = 1$, $r_w = r_m = 4$, $R_{0,w} = R_{0,m} = 5$.
  - weak selection scenario : $\beta_m = 6.3$, $\alpha_m = 1.6$, $r_m = 4.7$, $R_{0,m} = 3.9$.
  - strong selection scenario : $\beta_m = 40$, $\alpha_m = 20$, $r_m = 20$, $R_{0,m} = 2$.

  The grid size is 200 cells by 200 cells and the simulation all end at time $t = 12$.

Chapitre 4

Pulsating fronts for heterogeneous Fisher-KPP systems arising in evolutionary epidemiology

4.1 Introduction

This work is concerned with the heterogeneous reaction diffusion system

$$\begin{cases} \partial_t u = \partial_{xx} u + u\big[r_u(x) - \gamma_u(x)(u+v)\big] + \mu(x)v - \mu(x)u, & t>0,\, x\in\mathbb{R}, \\ \partial_t v = \partial_{xx} v + v\big[r_v(x) - \gamma_v(x)(u+v)\big] + \mu(x)u - \mu(x)v, & t>0,\, x\in\mathbb{R}, \end{cases} \tag{4.1}$$

where r_u, r_v are periodic functions and γ_u, γ_v, μ are periodic positive functions. After discussing the existence of nontrivial steady states via bifurcation technics, we construct pulsating fronts, despite the lack of comparison principle for (4.1). Before going into mathematical details, let us describe the relevance of the the above system in evolutionary epidemiology.

System (4.1) describes a theoretical population divided into two genotypes with respective densities $u(t,x)$ and $v(t,x)$, and living in a one dimensional habitat $x \in \mathbb{R}$. We assume that each genotype yields a different phenotype which also undergoes the influence of the environment. The difference in phenotype is expressed in terms of growth rate, mortality and competition, but we assume that the diffusion of the individuals is the same for each genotype. Finally, we take into account mutations occuring between the two genotypes.

The reaction coefficients r_u and r_v represent the intrinsic growth rates, which depend on the environment and take into account both birth and death rates. Notice that r_u and r_v may take some negative values, in deleterious areas where the death rate is greater than the birth rate. Function μ corresponds to the mutation rate between the two species. It imposes a truly *cooperative* dynamics in the small populations regime, and couples the dynamics of the two species. In particular, one expects that, at least for small mutation rates, *mutation aids survival and coexistence.* We also make the assumption that the mutation process is symmetric. From the mathematical point of view, this simplifies some of the arguments we use and improves the readability of the paper. We have no doubt that similar results hold in the non-symmetric case, though the proofs may be more involved.

In this context, the ability of the species to survive *globally in space* depends on the sign of the principal eigenvalue of the linearized operator around extinction $(0, 0)$, as we will show further, which involves the coefficients r_u, r_v, μ.

Finally, γ_u and γ_v represent the strength of the competition (for e.g. a finite resource) between the two strains. The associated dynamics arises when populations begin to grow. It has no influence on the survival of the two species, but regulates the equilibrium densities of the two populations.

Such a framework is particularly suited to model the propagation of a pathogenic species within a population of hosts. Indeed system (4.1) can easily be derived from a host-pathogen microscopic model [115] in which we neglect the influence of the pathogen on the host's diffusion.

In a homogeneous environment the role of mutations, allowing survival for both u and v, has recently been studied by Griette and Raoul [114], through the system

$$\begin{cases} \partial_t u = \partial_{xx} u + u(1 - (u + v)) + \mu(v - u) \\ \partial_t v = \partial_{xx} v + rv\left(1 - \dfrac{u + v}{K}\right) + \mu(u - v). \end{cases}$$

On the other hand, it is known that the spatial structure has a great influence on host-parasites systems, both at the epidemiological and evolutionary levels [33, 13, 147]. In order to understand the influence of heterogeneities, we aim at studying steady states and propagating solutions, or *fronts*, of system (4.1).

Traveling fronts in homogeneous environments. In a homogeneous environment, propagation in reaction diffusion equations is typically described by *traveling waves*, namely solutions to the parabolic equation consisting of a constant profile shifting at a constant speed. This goes back to the seminal works [89, 141] on the Fisher-KPP equation

$$\partial_t u = \Delta u + u(1 - u),$$

a model for the spreading of advantageous genetic features in a population. The literature on traveling fronts for such homogeneous reaction diffusion equations is very large, see [89, 141, 11, 12, 88, 99, 26] among others. In such situations, many techniques based on the comparison principle — such as some monotone iterative schemes or the sliding method [27]— can be used to get *a priori* bounds, existence and monotonicity properties of the solution.

Nevertheless, when considering nonlocal effects or systems, the comparison principle may no longer be available so that the above techniques do not apply and the situation is more involved. One usually uses topological degree arguments to construct traveling wave solutions: see [25, 84, 3, 125] for the nonlocal Fisher-KPP equation, [6] for a bistable nonlocal equation, [5] for a nonlocal equation in an evolutionary context, [114] for a homogeneous system in an evolutionary context... Notice also that the boundary conditions are then typically understood in a weak sense, meaning that the wave connects 0 to "something positive" that cannot easily be identified: for example, in the nonlocal Fisher-KPP equation the positive steady state $u \equiv 1$ may present a Turing instability.

In a heterogeneous environment, however, it is unreasonable to expect the existence of such a solution. The particular type of propagating solution we aim at constructing in our periodic case is the so called *pulsating front*, first introduced by Xin [205] in the framework of flame propagation.

Pulsating fronts in heterogeneous environments. The definition of a pulsating front is the natural extension, in the periodic framework, of the aforementioned traveling waves. We introduce a speed c and shift the origin with this speed to catch the asymptotic dynamics. Technically, a *pulsating front* (with speed c) is then a profile $(U(s,x), V(s,x))$ that is periodic in the space variable x, and that connects $(0,0)$ to a non-trivial state, such that $(u(t,x), v(t,x)) := (U(x-ct,c), V(x-ct,x))$ solves (4.1). Equivalently, a pulsating front is a solution of (4.1) connecting $(0,0)$ to a non-trivial state, and that satisfies the constraint

$$\left(u\left(t+\frac{L}{c},x\right), v\left(t+\frac{L}{c},x\right)\right) = (u(t,x-L), v(t,x-L)), \quad \forall (t,x) \in \mathbb{R}^2.$$

As far as monostable pulsating fronts are concerned, we refer among others to the seminal works of Weinberger [203], Berestycki and Hamel [18]. Let us also mention [133, 20, 120, 126] for related results.

One of the main difficulties we encounter when studying system (4.1) is that two main dynamics co-exist. On the one hand, when the population is small, (4.1) behaves like a cooperative system which enjoys a comparison principle. On the other hand, when the population is near a non-trivial equilibrium, (4.1) is closer to a competitive system. Since those dynamics cannot be separated, our system does not admit any comparison principle, and standard techniques such as monotone iterations cannot be applied. As far as we know, the present work is the first construction of pulsating fronts in a KPP situation (see [59, 130] for an ignition type nonlinearity) where comparison arguments are not available.

4.2 Main results and comments

4.2.1 Assumptions, linear material and notations

Periodic coefficients. Throughout this work, and even if not recalled, we always make the folllowing assumptions. Functions $r_u, r_v, \gamma_u, \gamma_v, \mu : \mathbb{R} \to \mathbb{R}$ are smooth and periodic with period $L > 0$. We assume further that γ_u, γ_v and μ are positive. We denote their bounds

$$\begin{array}{rcc}0 < & \gamma^0 \leq & \gamma_u(x), \gamma_v(x) & \leq \gamma^\infty \\ 0 < & \mu^0 \leq & \mu(x) & \leq \mu^\infty \\ & r^0 \leq & r_u(x), r_v(x) & \leq r^\infty,\end{array}$$

for all $x \in \mathbb{R}$. Notice that r_u and r_v are allowed to take negative values, which is an additional difficulty, in particular in the proofs of Lemma 4.4.3 and Lemma 4.5.4. The fact that r_u, r_v do not have a positive lower bound is the main reason why we need to introduce several types of eigenvalue problems, see (4.19) and (4.34), to construct subsolutions of related problems.

On the linearized system around $(0,0)$. We denote by A the symmetric matrix field arising after linearizing system (4.1) near the trivial solution $(0,0)$, namely

$$A(x) := \begin{pmatrix} r_u(x) - \mu(x) & \mu(x) \\ \mu(x) & r_v(x) - \mu(x) \end{pmatrix}. \tag{4.2}$$

Since $A(x)$ has positive off-diagonal coefficients, the elliptic system associated with the linear operator $-\Delta - A(x)$ is cooperative, *fully coupled* and therefore satisfies the strong maximum principle as well as other convenient properties [55].

Remark 4.2.1 (Cooperative elliptic systems and comparison principle). Cooperative systems enjoy similar comparison properties as scalar elliptic operators. In particular, [55] and [67] show that the maximum principle holds for cooperative systems if the principal eigenvalue is positive. Moreover, Section 13 (see also the beginning of Section 14) of [55] shows that, for so-called *fully coupled systems* (which is the case of all the operators we will encounter since $\mu(x) \geq \mu^0 > 0$), the converse holds. These facts will be used for instance in the proof of Lemma 4.4.2.

Let us now introduce a principal eigenvalue problem that is necessary to enunciate our main results.

Definition 4.2.2 (Principal eigenvalue)**.** We denote by λ_1 the principal eigenvalue of the stationary operator $-\Delta - A(x)$ with periodic conditions, where A is defined in (4.2).

In particular, we are equipped through this work with a principal eigenfunction $\Phi := \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ satisfying

$$\begin{cases} -\Phi_{xx} - A(x)\Phi = \lambda_1 \Phi \\ \Phi \text{ is } L\text{-periodic}, \quad \Phi \text{ is positive}, \quad \|\Phi\|_{\mathbf{L}^\infty} = 1. \end{cases} \tag{4.3}$$

For more details on principal eigenvalue for systems, we refer the reader to [55], in particular to Theorem 13.1 (Dirichlet boundary condition) which provides the principal eigenfunction. Furthermore, in the case of symmetric (self-adjoint) systems as the one we consider, the equivalent definition [67, (2.14)] provides some additional properties, in particular that the eigenfunction minimizes the Rayleigh quotient.

Function spaces. To avoid confusion with the usual function spaces, we denote the function spaces on a couple of functions with a bold font. Hence $\mathbf{L}^p(\Omega) := L^p(\Omega) \times L^p(\Omega)$ for $p \in [1,\infty]$ and $\mathbf{H}^q(\Omega) := H^q(\Omega) \times H^q(\Omega)$ for $q \in \mathbb{N}$ are equipped with the norms

$$\left\| \begin{pmatrix} u \\ v \end{pmatrix} \right\|_{\mathbf{L}^p} := \left\| \begin{pmatrix} \|u\|_{L^p} \\ \|v\|_{L^p} \end{pmatrix} \right\|_p, \quad \left\| \begin{pmatrix} u \\ v \end{pmatrix} \right\|_{\mathbf{H}^q} := \left\| \begin{pmatrix} \|u\|_{H^q} \\ \|v\|_{H^q} \end{pmatrix} \right\|_2.$$

Similarly, $\mathbf{C}^{\alpha,\beta} := C^{\alpha,\beta} \times C^{\alpha,\beta}$ for $\alpha \in \mathbb{N}$ and $\beta \in [0,1]$ is equipped with $\left\| \begin{pmatrix} u \\ v \end{pmatrix} \right\|_{\mathbf{C}^{\alpha,\beta}} := \max\left(\|u\|_{C^{\alpha,\beta}}, \|v\|_{C^{\alpha,\beta}}\right)$ and $\mathbf{C}^\alpha := \mathbf{C}^{\alpha,0}$. The subscript of those spaces denotes a restriction to a subspace : $\mathbf{L}^p_{per}$, $\mathbf{H}^q_{per}$, $\mathbf{C}^0_{per}$, $\mathbf{C}^{0,1}_{per}$, $\mathbf{C}^1_{per}$ for L-periodic functions, $\mathbf{H}^1_0$ for functions that vanish on the boundary, etc. Those function spaces are Banach spaces, and $\mathbf{H}^1$, $\mathbf{H}^1_{per}$, $\mathbf{H}^1_0$, $\mathbf{L}^2$ and $\mathbf{L}^2_{per}$ have a canonical Hilbert structure.

4.2.2 Main results

As well-known in KPP situations, the sign of the principal eigenvalue λ_1 is of crucial importance for the fate of the population: we expect extinction when $\lambda_1 > 0$ and propagation (hence survival) when $\lambda_1 < 0$. To confirm this scenario, we first study the existence of a nontrivial nonnegative steady state of problem (4.1), that is a nontrivial nonnegative L-periodic solution to the system

$$\begin{cases} -p'' = (r_u(x) - \gamma_u(x)(p+q))p + \mu(x)q - \mu(x)p \\ -q'' = (r_v(x) - \gamma_v(x)(p+q))q + \mu(x)p - \mu(x)q. \end{cases} \tag{4.4}$$

Theorem 4.2.3 (On nonnegative steady states)**.** *If* $\lambda_1 > 0$ *then* $(0,0)$ *is the only nonnegative steady state of problem* (4.1)*.*

On the other hand, if $\lambda_1 < 0$ *then there exists a nontrivial positive steady state* $(p(x) > 0, q(x) > 0)$ *of problem* (4.1)*.*

Next we turn to the long time behavior of the Cauchy problem associated with (4.1). First, we prove extinction when the principal eigenvalue is positive.

Proposition 4.2.4 (Extinction)**.** *Assume* $\lambda_1 > 0$*. Let a nonnegative and bounded initial condition* $(u^0(x), v^0(x))$ *be given. Then, any nonnegative solution* $(u(t,x), v(t,x)))$ *of* (4.1) *starting from* $(u^0(x), v^0(x))$ *goes extinct exponentially fast as* $t \to \infty$*, namely*

$$\max\left(\|u(t,\cdot)\|_{L^\infty(\mathbb{R})}, \|v(t,\cdot)\|_{L^\infty(\mathbb{R})}\right) = O(e^{-\lambda_1 t}).$$

The proof of Proposition 4.2.4 is rather simple so we now present it. The cooperative parabolic system

$$\begin{cases} \partial_t \bar{u} = \partial_{xx}\bar{u} + (r_u(x) - \mu(x))\bar{u} + \mu(x)\bar{v} \\ \partial_t \bar{v} = \partial_{xx}\bar{v} + (r_v(x) - \mu(x))\bar{v} + \mu(x)\bar{u}, \end{cases} \tag{4.5}$$

enjoys the comparison principle, see [90, Theorem 3.2]. On the one hand, any nonnegative $(u(t,x), v(t,x))$ solution of (4.1) is a subsolution of (4.5). On the other hand one can check that $(M\varphi(x)e^{-\lambda_1 t}, M\psi(x)e^{-\lambda_1 t})$ — with (φ, ψ) the principal eigenfunction satisfying (4.3)— is a solution of (4.5) which is initially larger than (u^0, v^0), if $M > 0$ is sufficiently large. Conclusion then follows from the comparison principle.

The reverse situation $\lambda_1 < 0$ is much more involved. Since in this case we aim at controlling the solution from below, the nonlinear term in (4.1) has to be carefully estimated. When $\lambda_1 < 0$, as a strong indication that the species does invade the whole line, we are going to construct pulsating fronts for (4.1).

Definition 4.2.5 (Pulsating front)**.** A pulsating front for (4.1) is a speed $c > 0$ and a classical positive solution $(u(t,x), v(t,x))$ to (4.1), which satisfy the constraint

$$\begin{pmatrix} u(t+\frac{L}{c}, x) \\ v(t+\frac{L}{c}, x) \end{pmatrix} = \begin{pmatrix} u(t, x-L) \\ v(t, x-L) \end{pmatrix}, \quad \forall (t,x) \in \mathbb{R}^2, \tag{4.6}$$

and supplemented with the boundary conditions

$$\liminf_{t\to+\infty} \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} > \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \quad \lim_{t\to-\infty} \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}, \tag{4.7}$$

locally uniformly w.r.t. x.

Following [20], we introduce a new set of variables that correspond to the frame of reference that follows the front propagation, that is $(s, x) := (x - ct, x)$. In these new variables, system (4.1) transfers into

$$\begin{cases} -(u_{xx} + 2u_{xs} + u_{ss}) - cu_s = (r_u(x) - \gamma_u(x)(u+v))u + \mu(x)v - \mu(x)u \\ -(v_{xx} + 2v_{xs} + v_{ss}) - cv_s = (r_v(x) - \gamma_v(x)(u+v))v + \mu(x)u - \mu(x)v, \end{cases} \tag{4.8}$$

and the constraint (4.6) is equivalent to the L-periodicity in x of the solutions to (4.8). An inherent difficulty to this approach is that the underlying elliptic operator, see the left-hand side member of system (4.8), is degenerate. This requires to consider a regularization of the operator and to derive a series of *a priori* estimates that do not depend on the regularization, see [18] or [20]. In addition to this inherent difficulty, the problem under consideration (4.1) does not admit a comparison principle, in contrast with the previous results on pulsating fronts. Nevertheless, as in the traveling wave case, if we only require boundary conditions in a weak sense — see (4.7) in Definition 4.2.5— then we can construct a pulsating front for (4.1) when the underlying principal eigenvalue is negative. This is the main result of the present paper since, as far as we know, this is the first construction of a pulsating front in a KPP situation without comparison principle.

Theorem 4.2.6 (Construction of a pulsating front)**.** *Assume $\lambda_1 < 0$. Then there exists a pulsating front solution to* (4.1)*.*

As clear in our construction through the paper, the speed $c^* > 0$ of the pulsating front of Theorem 4.2.6 satisfies the bound

$$0 < c^* \leq \bar{c}^0 := \inf\{c \geq 0 : \exists \lambda > 0, \mu_{c,0}(\lambda) = 0\},$$

where $\mu_{c,0}(\lambda)$ is the first eigenvalue of the operator

$$S_{c,\lambda,0}\Psi := -\Psi_{xx} + 2\lambda\Psi_x + [\lambda(c-\lambda)Id - A(x)]\,\Psi$$

with L-periodic boundary conditions. In previous works on pulsating fronts [203, 18, 20], it is typically proved that $\bar{c}^0$ is actually the minimal speed of pulsating fronts (and that faster pulsating fronts $c > \bar{c}^0$ also exist). Nevertheless, those proofs seem to rely deeply on the fact that pulsating fronts, as in Definition 4.2.5, are increasing in time, which is far from obvious in our context without comparison. We conjecture that this remains true but, for the sake of conciseness, we leave it as an open question.

The paper is organized as follows. Section 4.3 is concerned with the proof of Theorem 4.2.3 on steady states. In particular the construction of nontrivial steady states requires an adaptation of some bifurcations results [173, 174, 65] that are recalled in Appendix, Section 4.6.1. The rest of the paper is devoted to the proof of Theorem 4.2.6, that is the construction of a pulsating front. We first consider in Section 4.4 an ε-regularization of the degenerate problem (4.8) in a strip, where existence of a solution is proved by a Leray-Schauder topological degree argument. Then, in Section 4.5 we let the strip tend to $\mathbb{R}^2$ and finally let the regularization ε tend to zero to complete the proof of Theorem 4.2.6. This requires, among others, a generalization to elliptic systems of a Bernstein-type gradient estimate performed in [19], which is proved in Appendix, Section 4.6.2.

4.3 Steady states

This section is devoted to the proof of Theorem 4.2.3. The main difficulty is to prove the existence of a positive steady state to (4.1) when $\lambda_1 < 0$. To do so, we shall use the bifurcation theory introduced in the context of Sturm-Liouville problems by Crandall and Rabinowitz [65, 173, 174]. Though an equivalent result may be obtained using a topological degree argument, this efficient theory shows clearly the relationship between the existence of solutions to the nonlinear problem and the sign of the principal eigenvalue of the linearized operator near zero.

We shall first state and prove an independent theorem that takes advantage of the Krein-Rutman theorem in the context of a bifurcation originating from the principal eigenvalue of an operator. We will then use this theorem to show the link between the existence of a non-trivial positive steady state for (4.1), and the sign of the principal eigenvalue defined in (4.3).

4.3.1 Bifurcation result, a topological preliminary

We first prove a general bifurcation theorem, interesting by itself, which will be used as an end-point of the proof of Theorem 4.2.3. It consists in a refinement of the results in [65, 174, 173], under the additional assumption that the linearized operator satisfies the hypotheses of the Krein-Rutman Theorem. Our contribution is to show that the set of nontrivial fixed points only "meets" $\mathbb{R} \times \{0\}$ at point $(\frac{1}{\lambda_1(T)}, 0)$, with $\lambda_1(T)$ the principal eigenvalue of the linearized operator T.

This theorem is independent from the rest of the paper and we will thus use a different set of notations.

Theorem 4.3.1 (Bifurcation under Krein-Rutman assumption)**.** *Let E be a Banach space. Let $C \subset E$ be a closed convex cone with nonempty interior $\mathrm{Int}\, C \neq \varnothing$ and of vertex 0, i.e. such that $C \cap -C = \{0\}$. Let*

$$\begin{array}{rccc} F: & \mathbb{R} \times E & \to & E \\ & (\alpha, x) & \mapsto & F(\alpha, x) \end{array}$$

be a continuous and compact operator, i.e. F maps bounded sets into rela-

tively compact ones. Let us define

$$\mathcal{S} := \overline{\{(\alpha, x) \in \mathbb{R} \times E \backslash \{0\} : F(\alpha, x) = x\}}$$

the closure of the set of nontrivial fixed points of F, and

$$\mathbb{P}_{\mathbb{R}}\mathcal{S} := \{\alpha \in \mathbb{R} : \exists x \in C \backslash \{0\}, (\alpha, x) \in \mathcal{S}\}$$

the set of nontrivial solutions in C.

Let us assume the following.

1. *$\forall \alpha \in \mathbb{R}$, $F(\alpha, 0) = 0$.*
2. *F is Fréchet differentiable near $\mathbb{R} \times \{0\}$ with derivative αT locally uniformly w.r.t. α, i.e. for any $\alpha_1 < \alpha_2$ and $\epsilon > 0$ there exists $\delta > 0$ such that*

$$\forall \alpha \in (\alpha_1, \alpha_2),\ \|x\| \leq \delta \Rightarrow \|F(\alpha, x) - \alpha T x\| \leq \epsilon \|x\|.$$

3. *T satisfies the hypotheses of Theorem 4.6.1 (Krein-Rutman), i.e. $T(C \backslash \{0\}) \subset \operatorname{Int} C$. We denote by $\lambda_1(T) > 0$ its principal eigenvalue.*
4. *$\mathcal{S} \cap (\{\alpha\} \times C)$ is bounded locally uniformly w.r.t. $\alpha \in \mathbb{R}$.*
5. *There is no fixed point on the boundary of C, i.e. $\mathcal{S} \cap (\mathbb{R} \times (\partial C \backslash \{0\})) = \varnothing$.*

Then, either $\left(-\infty, \frac{1}{\lambda_1(T)}\right) \subset \mathbb{P}_{\mathbb{R}}\mathcal{S}$ or $\left(\frac{1}{\lambda_1(T)}, +\infty\right) \subset \mathbb{P}_{\mathbb{R}}\mathcal{S}$.

Proof. Let us first give a short overview of the proof. Since λ_1 is a simple eigenvalue, we know from Theorem 4.6.2 that there exists a branch of nontrivial solutions originating from $\left(\frac{1}{\lambda_1}, 0\right)$. We will show that this branch is actually contained in $\mathbb{R} \times C$, thanks to Theorem 4.6.3. Since it cannot meet $\mathbb{R} \times \{0\}$ except at $\left(\frac{1}{\lambda_1}, 0\right)$, it has to be unbounded, which proves our result.

Let us define

$$\mathcal{S}_C := \overline{\{(\alpha, x) \in \mathbb{R} \times (C \backslash \{0\}) : F(\alpha, x) = x\}}$$

which is a subset of $\mathcal{S}$, and $\alpha_1 := \frac{1}{\lambda_1(T)}$. We may call $(\alpha, x) \in \mathcal{S}_C$ a *degenerate* solution if $x \in \partial C$, and a *proper* solution otherwise.

Our first task is to show that the only degenerate solution is $\{(\alpha_1, 0)\}$. We first show $\mathcal{S}_C \cap (\mathbb{R} \times \partial C) \subset \{(\alpha_1, 0)\}$. Let $(\alpha, x) \in \mathcal{S}_C \cap (\mathbb{R} \times \partial C)$ be given. By item 5 we must have $x = 0$. Let $(\alpha_n, x_n) \to (\alpha, 0)$ such that $x_n \in C \setminus \{0\}$ and $F(\alpha_n, x_n) = x_n$. Let us define $y_n = \frac{x_n}{\|x_n\|} \in C \setminus \{0\}$. On the one hand since y_n is a bounded sequence and T is a compact operator, up to an extraction the sequence (Ty_n) converges to some z which, by item 3, must belong to C. On the other hand

$$y_n = \frac{x_n}{\|x_n\|} = \alpha_n T y_n + \frac{F(\alpha_n, x_n) - \alpha_n T x_n}{\|x_n\|} = \alpha z + o(1)$$

in virtue of items 1 and 2, so that in particular $z \neq 0$ and $\alpha \neq 0$. Since $y_n \to \alpha z$ and $Ty_n \to z$ we have $z = \alpha T z$. Hence $z \in C \setminus \{0\}$ is an eigenvector for T associated with the eigenvalue $\frac{1}{\alpha}$ so that Theorem 4.6.1 (Krein-Rutman) enforces $\alpha = \frac{1}{\lambda_1(T)} = \alpha_1$.

Next we aim at showing the reverse inclusion, that is $\{(\alpha_1, 0)\} \subset \mathcal{S}_C \cap (\mathbb{R} \times \partial C)$. We shall use the topological results of Appendix 4.6.1, namely Theorem 4.6.2 and Theorem 4.6.3. Let $z \in C$ be the eigenvector of T associated with $\lambda_1(T)$ such that $\|z\| = 1$, T^* the dual of T, and $l \in E'$ the eigenvector[1] of T^* associated with $\lambda_1(T)$ such that $\langle l, z \rangle = 1$, where $\langle \cdot, \cdot \rangle$ denotes the duality between E and its dual E'.

Now, for $\xi > 0$ and $\eta \in (0, 1)$, let us define

$$K^+_{\xi,\eta} := \{(\alpha, x) \in \mathbb{R} \times E : |\alpha - \alpha_1| < \xi, \langle l, x \rangle > \eta \|x\|\}.$$

The above sets are used to study the local properties of $\mathcal{S}$ near the branching point $(\alpha_1, 0)$. More precisely, it follows from Theorem 4.6.3 that $\mathcal{S} \backslash \{(\alpha_1, 0)\}$ contains a nontrivial connected component $\mathcal{C}^+_{\alpha_1}$ which is included in $K^+_{\xi,\eta}$ and near $(\alpha_1, 0)$:

$$\forall \xi > 0, \forall \eta \in (0, 1), \exists \zeta_0 > 0, \forall \zeta \in (0, \zeta_0),\, (\mathcal{C}^+_{\alpha_1} \cap B_\zeta) \subset K^+_{\xi,\eta},$$

where

$$B_\zeta = \{(\alpha, x) \in \mathbb{R} \times E : |\alpha - \alpha_1| < \zeta, \|x\| < \zeta\}.$$

Moreover, $\mathcal{C}^+_{\alpha_1}$ satisfies either item 1 or 2 in Theorem 4.6.2. Let us show that $(\mathcal{C}^+_{\alpha_1} \cap B_\zeta) \subset \mathbb{R} \times C$ for $\zeta > 0$ small enough, i.e.

$$\exists \zeta > 0, (\mathcal{C}^+_{\alpha_1} \cap B_\zeta) \subset \mathbb{R} \times C. \tag{4.9}$$

To do so, assume by contradiction that there exists a sequence $(\alpha^n, x_n) \to (\alpha_1, 0)$ such that

$$\forall n \in \mathbb{N}, (\alpha^n, x_n) \in \mathcal{C}^+_{\alpha_1} \text{ and } x_n \notin C.$$

Writing $\frac{x_n}{\|x_n\|} = \alpha^n T \frac{x_n}{\|x_n\|} + \frac{F(\alpha^n, x_n) - \alpha^n T x_n}{\|x_n\|}$ and reasoning as above, we see that (up to extraction) the sequence $\left(\frac{x_n}{\|x_n\|}\right)$ converges to some w such that $Tw = \frac{1}{\alpha_1} w = \lambda_1(T) w$. As a result $w = z$ or $w = -z$ (recall that z is the

[1] Let us recall that according to the Fredholm alternative, we have $\dim \ker(I - \lambda T) = \dim \ker(I - \lambda T^*) < \infty$ so that each eigenvalue of T is an eigenvalue of T^* with the same multiplicity.

unique eigenvector of T such that $z \in C$ and $\|z\| = 1$). But the property $\langle l, x_n \rangle \geq \eta \|x_n\|$ enforces $\frac{x_n}{\|x_n\|} \to z$. Since $\frac{x_n}{\|x_n\|} \notin C$ and $z \in Int\, C$, this is a contradiction. Hence (4.9) is proved.

Since $\mathcal{C}^+_{\alpha_1}$ is connected and $\mathcal{C}^+_{\alpha_1} \cap (\mathbb{R} \times \partial C) = \varnothing$ by item 5, we deduce from (4.9) that $\mathcal{C}^+_{\alpha_1} \subset \mathcal{S}_C$. Moreover, since by definition $\{(\alpha_1, 0)\} \in \overline{\mathcal{C}^+_{\alpha_1}}$ and $\mathcal{S}_C$ is closed, we have

$$\{(\alpha_1, 0)\} \subset \mathcal{S}_C \cap (\mathbb{R} \times \partial C).$$

We have then established that $\{(\alpha_1, 0)\}$ is the only degenerate solution in C i.e. $\mathcal{S}_C \cap (\mathbb{R} \times \partial C) = \{(\alpha_1, 0)\}$. Applying Theorem 4.6.3 near $\{(\alpha_1, 0)\}$, there exists a branch $\mathcal{C}^+_{\alpha_1}$ of solutions such that $\{(\alpha_1, 0)\} \subset \overline{\mathcal{C}^+_{\alpha_1}}$. By the above argument, $\mathcal{C}^+_{\alpha_1} \subset \mathcal{S}_C$. Since $\mathcal{C}^+_{\alpha_1}$ cannot meet $\mathbb{R} \times \{0\}$ at $(\alpha, 0) \neq (\alpha_1, 0)$, it follows from Theorem 4.6.3 that $\mathcal{C}^+_{\alpha_1}$ is unbounded. It therefore follows from item 4 that there exists a sequence $(\alpha^n, x^n) \in \mathcal{C}^+_{\alpha_1}$ with $|\alpha^n| \to \infty$. Since $\mathcal{C}^+_{\alpha_1}$ contains only proper solutions (i.e. $\mathcal{C}^+_{\alpha_1} \cap (\mathbb{R} \times \partial C) = \varnothing$), the projection $P_{\mathbb{R}}(\mathcal{C}^+_{\alpha_1})$ of $\mathcal{C}^+_{\alpha_1}$ on $\mathbb{R}$ is included in $\mathbb{P}_{\mathbb{R}}\mathcal{S}$. Finally, the continuity of the projection $P_{\mathbb{R}}$ and the fact that $\mathcal{C}^+_{\alpha_1}$ is connected show that either $(\alpha_1, \alpha^n) \subset P_{\mathbb{R}}(\mathcal{C}^+_{\alpha_1})$ or $(\alpha^n, \alpha_1) \subset P_{\mathbb{R}}(\mathcal{C}^+_{\alpha_1})$, depending on $\alpha_1 \leq \alpha^n$ or $\alpha^n \leq \alpha_1$. Letting $n \to \infty$ proves Theorem 4.3.1. □

4.3.2 A priori estimates on steady states

In order to meet the hypotheses of Theorem 4.3.1 in subsection 4.3.3, we prove some *a priori* estimates on stationary solutions. We have in mind to apply Theorem 4.3.1 in the cone of nonnegativity of $\mathbf{L}^\infty_{per}(\mathbb{R})$. Specifically, Lemma 4.3.2 will be used to meet item 4 (the solutions are locally bounded), and Lemma 4.3.3 will be used to meet item 5 (there is no solution on the boundary of the cone).

Lemma 4.3.2 (Uniform upper bound)**.** *There exists a positive constant $C = C(r^\infty, \mu^\infty, \gamma^0)$ such that any nonnegative periodic solution (p, q) to (4.4) satisfies $p(x) \leq C$ and $q(x) \leq C$, for all $x \in \mathbb{R}$.*

Proof. Let $\begin{pmatrix} p \\ q \end{pmatrix}$ be a solution to system (4.4), so that

$$\left\{ \begin{array}{lll} -p'' & \leq & p(r_u - \gamma_u p) + q(\mu - \gamma_u p) \\ -q'' & \leq & q(r_v - \gamma_v q) + p(\mu - \gamma_v q). \end{array} \right. \tag{4.10}$$

Let us define $C := \max\left(\frac{r^\infty}{\gamma^0}, \frac{\mu^\infty}{\gamma^0}\right) > 0$. Denote by x_0 a point where p reaches its maximum, so that $-p''(x_0) \geq 0$. Assume by contradiction that $p(x_0) > C$. Then, in virtue of (4.10), one has $-p''(x_0) \leq p(x_0)(r_u(x_0) - \gamma_u(x_0)C) < 0$, which is a contradiction. Thus $p \leq C$. Inequality $q \leq C$ is proved the same way. □

Lemma 4.3.3 (Positivity of solutions)**.** *Any nonnegative periodic solution (p, q) to (4.4) such that $(p, q) \not\equiv (0, 0)$ actually satisfies $p(x) > 0$ and $q(x) > 0$, for all $x \in \mathbb{R}$.*

Proof. Write

$$\begin{cases} -p'' & \geq & p(r_u - \mu - \gamma_u(p+q)) \\ -q'' & \geq & q(r_v - \mu - \gamma_v(p+q)), \end{cases}$$

and the result is a direct application of the strong maximum principle. □

4.3.3 Proof of the result on steady states

We are now in the position to prove Theorem 4.2.3.

The $\lambda_1 > 0$ case. Let (p, q) be a nonnegative steady state solving (4.4). We need to show that $(p, q) \equiv (0, 0)$. Let us recall that $\Phi = \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ is the principal eigenfunction solving (4.3). From Lemma 4.3.2, we can define

$$C_0 := \inf \left\{ C \geq 0 : \forall x \in \mathbb{R}, \begin{pmatrix} p(x) \\ q(x) \end{pmatrix} \leq C \begin{pmatrix} \varphi(x) \\ \psi(x) \end{pmatrix} \right\}. \tag{4.11}$$

Let us assume by contradiction that $C_0 > 0$. Hence, without loss of generality, $p - C_0\varphi$ attains a zero maximum value at some point $x_0 \in \mathbb{R}$, and $q - C_0\psi \leq 0$ at this point. But, from (4.3) and (4.4) we get

$$\begin{cases} -(p - C_0\varphi)'' - (r_u(x) - \mu(x))(p - C_0\varphi) = \mu(x)(q - C_0\psi) - \gamma_u(p+q)p \\ \hfill -\lambda_1 C_0 \varphi < 0 \\ -(q - C_0\psi)'' - (r_v(x) - \mu(x))(q - C_0\psi) = \mu(x)(p - C_0\varphi) - \gamma_v(p+q)q \\ \hfill -\lambda_1 C_0 \psi < 0. \end{cases}$$

Evaluating the first inequality at point x_0 yields $(p - C_0\varphi)''(x_0) > 0$, which is a contradiction since x_0 is a local maximum for $p - C_0\varphi$. As a result $C_0 = 0$ and $(p, q) \equiv (0, 0)$. □

The reverse situation $\lambda_1 < 0$, where we need to prove the existence of a nontrivial steady state, is more involved. We shall combine our *a priori* estimates of subsection 4.3.2 with our bifurcation result, namely Theorem 4.3.1. We will also use the $\lambda_1 > 0$ case. We want to stress eventually that we will use the notations introduced in subsection 4.2.1, in particular for functional spaces.

Before starting the proof itself, we would like to present briefly the core of the argument we use. We introduce a new parameter $\beta \in \mathbb{R}$ and look at the modified system

$$\begin{cases} -p'' & = & p(r_u + \beta - \gamma_u(p+q)) + \mu(q-p) \\ -q'' & = & q(r_v + \beta - \gamma_v(p+q)) + \mu(p-q) \end{cases} \tag{4.12}$$

which is system (4.4) with r_u (resp. r_v) replaced by $r_u + \beta$ (resp. $r_v + \beta$). We apply Theorem 4.3.1 to system (4.12) with the bifurcation parameter β. There exists then a branch of solutions originating from $\beta = \lambda_1$, and which spans to $\beta \to +\infty$ since the eigenvalue of the linearization of system (4.12) is *positive* for $\beta < \lambda_1$ (i.e. no solution exists for $\beta \in (-\infty, \lambda_1)$). In particular there exists a solution for $\beta = 0$ since $\lambda_1 < 0$. Let us make this argument rigorous.

The $\lambda_1 < 0$ case. We start with the following lemma.

Lemma 4.3.4 (Fréchet differentiability)**.** *Let*

$$f \begin{pmatrix} p \\ q \end{pmatrix} := \begin{pmatrix} -\gamma_u(p+q)p \\ -\gamma_v(p+q)q \end{pmatrix}.$$

Then, the induced operator $\mathbf{L}^\infty_{per}(\mathbb{R}) \longrightarrow \mathbf{L}^\infty_{per}(\mathbb{R})$ is Fréchet differentiable at $\begin{pmatrix} 0 \\ 0 \end{pmatrix}$ with derivative $0_{\mathbf{L}^\infty}$.

Proof. We need to show that

$$\left\| f \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} = o\left(\left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \right)$$

as $\left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \to 0$. We have

$$\left\| f \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \leq \gamma^\infty \left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} \|p+q\|_{L^\infty_{per}(\mathbb{R})} \leq 2\gamma^\infty \left\| \begin{pmatrix} p \\ q \end{pmatrix} \right\|^2_{\mathbf{L}^\infty_{per}(\mathbb{R})}$$

which proves the lemma. □

We are now in the position to complete the proof of Theorem 4.2.3. It follows from classical theory that, for $M > 0$ large enough, the problem

$$\begin{cases} -\begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix}'' - A(x) \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix} + M \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix} = \begin{pmatrix} p \\ q \end{pmatrix} \\ \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix} \in \mathbf{H}^1_{per} \end{cases} \tag{4.13}$$

has a unique weak solution $\begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix}$, for each $\begin{pmatrix} p \\ q \end{pmatrix} \in \mathbf{L}^2_{per}$. Let us call L_M^{-1} the associated operator, namely

$$\begin{array}{rccc} L_M^{-1}: & \mathbf{L}^2_{per} & \to & \mathbf{H}^1_{per} \\ & \begin{pmatrix} p \\ q \end{pmatrix} & \mapsto & \begin{pmatrix} \tilde{p} \\ \tilde{q} \end{pmatrix}. \end{array}$$

Notice that, assuming $M > -\lambda_1$, the principal eigenvalue associated with problem (4.13) is $\lambda_1' := \lambda_1 + M > 0$, and recall that the actual algebraic eigenvalue $\lambda_1(L_M^{-1})$ of the operator L_M^{-1} is given by

$$\lambda_1(L_M^{-1}) = \frac{1}{\lambda_1'} > 0.$$

From elliptic regularity, the restriction of L_M^{-1} to $\mathbf{L}^\infty_{per}(\mathbb{R})$ maps $\mathbf{L}^\infty_{per}(\mathbb{R})$ into $\mathbf{C}^{0,\theta}_{per}(\mathbb{R})$, $0 < \theta < 1$, and L_M^{-1} is therefore a compact operator on $\mathbf{L}^\infty_{per}(\mathbb{R})$. Hence,

$$\begin{array}{rccl} F: & \mathbb{R} \times \mathbf{L}^\infty_{per}(\mathbb{R}) & \to & \mathbf{L}^\infty_{per}(\mathbb{R}) \\ & \left(\alpha, \begin{pmatrix} p \\ q \end{pmatrix}\right) & \mapsto & L_M^{-1}\left(f\begin{pmatrix} p \\ q \end{pmatrix} + \alpha \begin{pmatrix} p \\ q \end{pmatrix}\right) \end{array}$$

is a continuous and compact map, to which we aim at applying Theorem 4.3.1. Let us recall that the cone of nonegativity

$$C := \left\{ \begin{pmatrix} p \\ q \end{pmatrix} \in \mathbf{L}^\infty_{per}(\mathbb{R}) : \begin{pmatrix} p \\ q \end{pmatrix} \geq \begin{pmatrix} 0 \\ 0 \end{pmatrix} \right\}$$

is, as required by Theorem 4.3.1, a closed convex cone of vertex 0 and nonempty interior in $\mathbf{L}^\infty_{per}$. Finally, we want to stress that solutions to $F\left(\alpha, \begin{pmatrix} p \\ q \end{pmatrix}\right) = \begin{pmatrix} p \\ q \end{pmatrix}$ are classical solutions to the system

$$-\begin{pmatrix} p \\ q \end{pmatrix}'' - A(x)\begin{pmatrix} p \\ q \end{pmatrix} = f\begin{pmatrix} p \\ q \end{pmatrix} + (\alpha - M)\begin{pmatrix} p \\ q \end{pmatrix} \tag{4.14}$$

which is equivalent to system (4.12) with $\beta = \alpha - M$, where α is the bifurcation parameter. Let us check that all assumptions of Theorem 4.3.1 are satisfied.

1. Clearly we have $\forall \alpha \in \mathbb{R}, F\left(\alpha, \begin{pmatrix} 0 \\ 0 \end{pmatrix}\right) = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$.

2. From Lemma 4.3.4 and the composition rule for derivatives, F is Fréchet differentiable near $\mathbb{R} \times \left\{\begin{pmatrix} 0 \\ 0 \end{pmatrix}\right\}$ with derivative αL_M^{-1} locally uniformly w.r.t. α.

3. From the comparison principle (available for L_M^{-1} since $\lambda_1' > 0$, see [55]), L_M^{-1} satisfies the hypotheses of the Krein-Rutman Theorem, namely $L_M^{-1}(C \setminus \{0\}) \subset Int\, C$.

4. Lemma 4.3.2 shows that, for any $\alpha_* < \alpha^*$, $\mathcal{S} \cap (\alpha_*, \alpha^*) \times C$ is bounded (in view of system (4.12), the constant C defined in the proof of Lemma 4.3.2 is locally bounded w.r.t. α).

5. From Lemma 4.3.3, any nonnegative fixed point is positive, i.e. $\mathcal{S} \cap (\mathbb{R} \times (\partial C \setminus \{0\})) = \varnothing$.

We may now apply Theorem 4.3.1 which states that either $\mathcal{S} \cap (\{\alpha\} \times (C \setminus \{0\})) \neq \varnothing$ for any $\alpha \in (\lambda_1', +\infty)$ or $\mathcal{S} \cap (\{\alpha\} \times (C \setminus \{0\})) \neq \varnothing$ for any $\alpha \in (-\infty, \lambda_1')$. Invoking the case of positive principal eigenvalue (see the begininning of the present subsection), we see that there is no nonnegative nontrivial fixed points when $\alpha < \lambda_1'$. As a result we have

$$\forall \alpha \in (\lambda_1', +\infty), \mathcal{S} \cap (\{\alpha\} \times (C \setminus \{0\})) \neq \varnothing.$$

In particular, since $\lambda_1' = M + \lambda_1 < M$, there exists a positive fixed point for $\alpha = M$, which is a classical solution of (4.14). This completes the proof of Theorem 4.2.3. □

4.4 Towards pulsating fronts: the problem in a strip

We have established above the existence of a nontrivial periodic steady state $(p(x) > 0, q(x) > 0)$ when the first eigenvalue of the linearized stationary problem λ_1 is negative. The rest of the paper is devoted to the construction of a pulsating front, see Definition 4.2.5, when $\lambda_1 < 0$.

In order to circumvent the degeneracy of the elliptic operator in (4.8) we need to introduce a regularization via a small positive parameter ε. Also, in order to gain compactness, the system (4.8) posed in $(s, x) \in \mathbb{R}^2$ (recall that $s = x - ct$) is first reduced to a strip $(s, x) \in (-a, a) \times \mathbb{R}$ (recall the periodicity in the x variable).

More precisely, let us first define the constants $a_0^* > 0$ (minimal size of the strip in the s variable on which we impose a normalization), $\nu_0 > 0$ (maximal normalization), and $K_0 > 0$ by

$$a_0^* := 2\sqrt{\frac{5}{-\lambda_1}}, \qquad \nu_0 := \min\left(1, \frac{-\lambda_1}{4\gamma^\infty}, \min_{x\in\mathbb{R}}(p(x), q(x))\right),$$

$$K_0 := \max\left(\frac{8\gamma^\infty \max_{x\in\mathbb{R}}(p(x) + q(x))}{-\lambda_1}, 1 + \max_{x\in\mathbb{R}}\left(\frac{p(x)}{q(x)}, \frac{q(x)}{p(x)}\right)\right).$$

Also we define the strip $\Omega_0 := (-a_0, a_0) \times \mathbb{R}$ for $a_0 \geq a_0^*$.

Theorem 4.4.1 (A solution of the regularized problem in a strip)**.** *Assume $\lambda_1 < 0$. Let $a_0 > a_0^*$, $0 < \nu < \nu_0$ and $K > K_0$ be given. Then there is $C > 0$ such that, for any $\varepsilon \in (0, 1)$, there is $\bar{a} = \bar{a}^\varepsilon > 0$ (whose definition can be found in Lemma 4.4.3 item 4) such that: for any $a \geq a_0 + \bar{a}$, there exist a L-periodic in x and positive $(u(s, x), v(s, x))$, bounded by C, and a speed*

$c \in (0, \bar{c}^\varepsilon + \varepsilon)$, solving the following mixed Dirichlet-periodic problem on the domain $\Omega := (-a, a) \times \mathbb{R}$

$$\begin{cases} L_\varepsilon u - cu_s = u(r_u - \gamma_u(u+v)) + \mu v - \mu u & \text{in } \Omega \\ L_\varepsilon v - cv_s = v(r_v - \gamma_v(u+v)) + \mu u - \mu v & \text{in } \Omega \\ (u,v)(-a,x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\ (u,v)(a,x) = (0,0), \quad \forall x \in \mathbb{R} \\ \sup\limits_{\Omega_0} \, (u+v) = \nu, \end{cases} \tag{4.15}$$

where $L_\varepsilon := -\partial_{xx} - 2\partial_{xs} - (1+\varepsilon)\partial_{ss}$ and the speed $\bar{c}^\varepsilon \geq 0$ is defined in Lemma 4.4.2.

This whole section is concerned with the proof of Theorem 4.4.1. In order to use a topological degree argument, we transform continuously our problem until we get a simpler problem for which we know how to compute the degree explicitely.

Our first homotopy allows us to get rid of the competitive behaviour of the system. Technically we interpolate the nonlinear terms $-\gamma_u uv$, $-\gamma_v uv$ with the linear terms $-\gamma_u u \frac{q}{K}$, $-\gamma_v v \frac{p}{K}$ respectively, to obtain system (4.20) which is truly cooperative. In particular, since the boundary condition at $s = -a$ is a supersolution to (4.20), we can prove the existence of a unique solution to (4.20) for each $c \in \mathbb{R}$ via a monotone iteration technique, the monotonicity of the constructed solutions and further properties. Nevertheless we still need to compute the degree explicitely, to which end we use a second homotopy that interpolates the right-hand side of (4.20) with a linear term, and then a third homotopy to get rid of the coupling between the speed c and the profiles u and v. At this point we are equipped to compute the degree. For related arguments in a traveling wave context, we refer the reader to [25, 5, 6, 114].

The role of the a priori estimates in subsections 4.4.1, 4.4.2 and 4.4.3 is to ensure that there is no solution on the boundary of the open sets that we choose to contain our problem, and thus that the degree is a constant along our path. In subsection 4.4.4, we complete the proof of Theorem 4.4.1.

Before that, we need to establish some properties on the upper bound $\bar{c}^\varepsilon$ for the speed in Theorem 4.4.1.

Lemma 4.4.2 (On the upper bound for the speed)**.** *Let*

$$S_{c,\lambda,\varepsilon}\Psi := -\Psi_{xx} + 2\lambda\Psi_x + \left[\lambda(c - (1+\varepsilon)\lambda)Id - A(x)\right]\Psi,$$

and define

$$\bar{c}^\varepsilon = \inf\left\{c \geq 0, \exists \lambda > 0, \mu_{c,\varepsilon}(\lambda) = 0\right\}, \tag{4.16}$$

where $\mu_{c,\varepsilon}(\lambda)$ is the first eigenvalue of the operator $S_{c,\lambda,\varepsilon}$ with L-periodic boundary conditions. Then the following holds.

1. *For any* $\varepsilon \in (0,1)$, *we have* $\bar{c}^\varepsilon < +\infty$.

2. *We have* $\bar{c}^\varepsilon = \min\{c \geq 0, \exists \lambda > 0, \mu_{c,\varepsilon}(\lambda) = 0\}$.

3. $\varepsilon \mapsto \bar{c}^\varepsilon$ *is nondecreasing.*

Proof. 1. We need to prove that the set in the right-hand side of (4.16) is non-empty. We first notice that $\mu_{c,\varepsilon}(0) = \lambda_1 < 0$ for any $c > 0$. Next, for the eigenfunction $\Phi := \begin{pmatrix}\varphi\\ \psi\end{pmatrix}$ solving (4.3), we have $S_{c,\lambda,\varepsilon}\Phi = \lambda_1\Phi + 2\lambda\Phi_x + \lambda(c - (1+\varepsilon)\lambda)\Phi$. In particular for $\lambda = \frac{c}{2}$, we have

$$S_{c,\frac{c}{2},\varepsilon}\Phi \geq (\lambda_1 + \frac{c^2}{4}(1-\varepsilon))\Phi + c\Phi_x \geq \begin{pmatrix}0\\0\end{pmatrix}$$

as soon as $c \geq c_*$ where $c_* > 0$ depends only on the quantities $\min(\varphi,\psi)$, $\|\Phi_x\|_{\mathbf{L}^\infty}$ and $-\lambda_1$.

Recalling, see [55], that the eigenvalue is given by

$$\mu_{c_*,\varepsilon}\left(\frac{c_*}{2}\right) = \sup\left\{\rho \in \mathbb{R} : \exists \Psi \in \mathbf{C}^2_{per}, \Psi > 0, S_{c,\frac{c}{2},\varepsilon}\Psi - \rho\Psi \geq 0\right\},$$

it follows from the above that $\mu_{c_*,\varepsilon}\left(\frac{c_*}{2}\right) \geq 0$. Since the principal eigenvalue of $S_{c,\lambda,\varepsilon}$ is continuous[2] with respect to λ (and c), there exists $\lambda \in (0, \frac{c_*}{2}]$ such that $\mu_{c_*,\varepsilon}(\lambda) = 0$, which proves that (4.16) is well-posed.

2. For the eigenfunction Φ solving (4.3), we have

$$S_{c,\lambda,\varepsilon}\Phi \leq 2\lambda\Phi_x - \lambda^2\left(1 + \varepsilon - \frac{c}{\lambda}\right)\Phi < \begin{pmatrix}0\\0\end{pmatrix}$$

as soon as $\lambda \geq \lambda_*$ where $\lambda_* > 0$ depends only on $\min(\varphi,\psi)$, $\|\Phi_x\|_{\mathbf{L}^\infty}$, and an upper bound for c. Hence the maximum principle does not hold for $S_{c,\lambda,\varepsilon}$, and it follows from [55, Theorem 14.1] that $\mu_{c,\varepsilon}(\lambda) \leq 0$.

Now, we consider sequences $c_n \searrow \bar{c}^\varepsilon$, and $\lambda_n \geq 0$ such that $\mu_{c_n,\varepsilon}(\lambda_n) = 0$. From the above, we have $\lambda_n \leq \lambda_*$ so that, up to extraction, $\lambda_n \to \lambda_\infty$. From the continuity of the principal eigenvalue, we deduce that $\mu_{\bar{c}^\varepsilon,\varepsilon}(\lambda_\infty) = 0$, and the infimum in (4.16) is attained.

[2] This property is potentially false in general but has a simple proof in our setting. Take a sequence of operators $T_n \to T$ that send a proper cone C into $K \subset \mathrm{Int}\, C$ with K compact, i.e. $T_n(C) \subset K$ and $T(C) \subset K$. Assume that the series of normalized eigenvectors $x_n \in C$ s.t. $T_n x_n = \lambda_n x_n$ diverges, then we can extract to sequences $x_n^1 \to y \in C$ and $x_n^2 \to z \in C$ with $y \neq z$. Extracting further, there exists μ and ν s.t. $Ty = \mu y$ and $Tz = \nu z$ which is a contradiction since $y \neq z$. Hence the continuity of the eigenvalue.

3. Let $\varepsilon' \leq \varepsilon$ and $c > 0$ such that there is a positive solution Θ to $S_{c,\lambda,\varepsilon}\Theta = \begin{pmatrix}0\\0\end{pmatrix}$. Then $S_{c,\lambda,\varepsilon'}\Theta = (\varepsilon - \varepsilon')\lambda^2\Theta \geq \begin{pmatrix}0\\0\end{pmatrix}$ so that, as in the proof of item 1, there exists $0 < \lambda' \leq \lambda$ such that $\mu_{c,\varepsilon'}(\lambda') = 0$. Thus

$$\{c \geq 0, \exists\lambda > 0, \mu_{c,\varepsilon}(\lambda) = 0\} \subset \{c \geq 0, \exists\lambda > 0, \mu_{c,\varepsilon'}(\lambda) = 0\}.$$

Taking the infimum on c yields $\bar{c}^{\varepsilon'} \leq \bar{c}^{\varepsilon}$.

Lemma 4.4.2 is proved. □

4.4.1 Estimates along the first homotopy

Let us recall that the role of the first homotopy is to get rid of the competition of our original problem ($\tau = 1$), so that the classical comparison methods become available for $\tau = 0$. Notice that it is crucial that the Dirichlet condition at $s = -a$ is a supersolution for the $\tau = 0$ problem, in order to apply a sliding method in the following subsection. Hence, for $0 \leq \tau \leq 1$, we consider the problem

$$\begin{cases} L_\varepsilon u - cu_s = u[r_u - \gamma_u(u + (\tau v + (1-\tau)\frac{q}{K}))] + \mu v - \mu u \\ L_\varepsilon v - cv_s = v[r_v - \gamma_v((\tau u + (1-\tau)\frac{p}{K}) + v)] + \mu u - \mu v \\ (u,v)(-a,x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\ (u,v)(a,x) = (0,0), \quad \forall x \in \mathbb{R}, \end{cases} \tag{4.17}$$

along with the normalization condition $\sup_{\Omega_0}(u+v) = \nu$.

Lemma 4.4.3 (A priori estimates along the first homotopy)**.** *Let a nonnegative $(u,v) \in \mathbf{C}^1_{per}(\Omega)$ (where $\Omega = (-a,a) \times \mathbb{R}$ and the periodicity is understood only w.r.t. the $x \in \mathbb{R}$ variable) and $c \in \mathbb{R}$ solve* (4.17)*, with $0 \leq \tau \leq 1$. Then*

1. *(u,v) is a classical solution to* (4.17)*, i.e. $(u,v) \in \mathbf{C}^2(\overline{\Omega})$.*

2. *The positive constant $C := \max(\frac{2r^\infty}{\gamma^0}, K\max(p+q))$ is such that*

$$u(s,x) + v(s,x) \leq C, \quad \forall (s,x) \in \overline{\Omega} = [-a,a] \times \mathbb{R}.$$

3. *(u,v) is positive in Ω.*

4. *Let $\lambda_0 > 0$ and $\Phi_0(x) = \begin{pmatrix}\Phi_u(x)\\\Phi_v(x)\end{pmatrix} > \begin{pmatrix}0\\0\end{pmatrix}$ be such that $S_{\bar{c}^\varepsilon,\lambda_0,\varepsilon}\Phi_0 = 0$ and $\|\Phi_0\|_{\mathbf{L}^\infty_{per}(\mathbb{R})} = 1$. Define $\bar{a} = \bar{a}^\varepsilon := \max(-\frac{1}{\lambda_0}\ln\left(\frac{\nu\min(\Phi_u,\Phi_v)}{4K\max(p,q)}\right), 1)$. Then if $a \geq a_0 + \bar{a}$ and $c \geq \bar{c}^\varepsilon$, we have $\sup_{\Omega_0}(u+v) < \frac{\nu}{2}$.*

5. *If $c = 0$ and $a \geq a_0 + 1$ then*

$$\sup_{\Omega_0} (u+v) \geq \frac{-\lambda_1^\varepsilon}{\gamma^\infty} - \frac{\max(p+q)}{K}, \tag{4.18}$$

where λ_1^ε is the principal eigenvalue of the operator $L_\varepsilon - A(x)$ with Dirichlet condition in s and L-periodic condition in x, in the domain Ω_0, as defined in (4.19).

Proof. 1. This is true from classical elliptic regularity. We omit the details.

2. In view of (4.17), the sum $S := u + v$ satisfies

$$\begin{aligned} L_\varepsilon S - cS_s = r_u u + r_v v - \gamma_u u(u + (1-\tau)\frac{q}{K} + \tau v) \\ - \gamma_v v(v + (1-\tau)\frac{p}{K} + \tau u) \leq r^\infty S - \gamma^0(u^2+v^2). \end{aligned}$$

Since $S^2 = u^2 + 2uv + v^2 \leq 2(u^2+v^2)$, we have

$$L_\varepsilon S - cS_s \leq \frac{\gamma^0}{2} S \left(\frac{2r^\infty}{\gamma^0} - S \right).$$

Since the maximum principle holds for the operator $L_\varepsilon - c\partial_s$ independently of c and $\varepsilon > 0$, S cannot have an interior local maximum which is greater than $\frac{2r^\infty}{\gamma^0}$. This along with the boundary conditions $S(-a, x) = K(p(x) + q(x))$, $S(a, x) = 0$ proves item 2.

3. Assume that there exists $(s_0, x_0) \in (-a, a) \times \mathbb{R}$ such that $u(s_0, x_0) = 0$. Since

$$L_\varepsilon u - cu_s \geq u \left[r_u(x) - \gamma_u(x) \left(u + \left(\tau v + (1-\tau)\frac{q}{K} \right) \right) - \mu(x) \right],$$

the strong maximum principle enforces $u \equiv 0$ which contradicts the boundary condition at $s = -a$. The same argument applies to v.

4. Let $\zeta(s, x) := Be^{-\lambda_0 s}\Phi_0(x)$, $B > 0$. Then we have

$$\begin{aligned} L_\varepsilon \zeta - c\zeta_s = Be^{-\lambda_0 s}\left(S_{\bar{c}^\varepsilon, \lambda_0, \varepsilon}\Phi_0 + A(x)\Phi_0 + \lambda_0(c - \bar{c}^\varepsilon)\Phi_0\right) \\ = A(x)\zeta + \lambda_0(c - \bar{c}^\varepsilon)\zeta \geq A(x)\zeta, \end{aligned}$$

so that ζ is a strict supersolution to problem (4.17). By item 2, one can define

$$B_0 := \inf\left\{ B > 0, \forall (s,x) \in [-a, a] \times \mathbb{R}, \begin{pmatrix} u(s,x) \\ v(s,x) \end{pmatrix} \leq \zeta(s,x) \right\} > 0$$

and $\zeta_0(s,x) = \begin{pmatrix}\zeta_u(s,x)\\ \zeta_v(s,x)\end{pmatrix} := B_0 e^{-\lambda_0 s}\Phi_0(x)$. From the strong maximum principle in $(-a,a)\times\mathbb{R}$, and the $s=a$ boundary condition, the touching point has to lie on $s=-a$. Thus there exists x_0 such that either $\zeta_u(-a,x_0)=u(-a,x_0)$ or $\zeta_v(-a,x_0)=v(-a,x_0)$. In any case one has $B_0 \le K e^{-\lambda_0 a}\frac{\max(p,q)}{\min(\Phi_u,\Phi_v)}$, which in in turn implies

$$\begin{aligned}\sup_{\Omega_0}(u+v) \le 2B_0 e^{\lambda_0 a_0} &\le 2K\frac{\max(p,q)}{\min(\Phi_u,\Phi_v)}e^{-\lambda_0(a-a_0)}\\ &\le 2K\frac{\max(p,q)}{\min(\Phi_u,\Phi_v)}e^{-\lambda_0\bar a} \le \frac{\nu}{2},\end{aligned}$$

in view of the definition of $\bar a$. This proves item 4.

5. Assume by contradiction that $\sup_{\Omega_0}(u+v) < \frac{-\lambda_1^\varepsilon}{\gamma^\infty} - \frac{\max(p+q)}{K}$ (which in particular enforces $\lambda_1^\varepsilon<0$). Then, in $(-a_0,a_0)\times\mathbb{R}$, we have

$$\begin{cases} L_\varepsilon u &= (r_u-\mu-\gamma_u(u+\tau v+(1-\tau)\frac{q}{K}))u+\mu v\\ &\qquad \ge (r_u-\mu+\lambda_1^\varepsilon)u+\mu v,\\ L_\varepsilon v &= (r_v-\mu-\gamma_v(v+\tau u+(1-\tau)\frac{p}{K}))v+\mu u\\ &\qquad \ge (r_v-\mu+\lambda_1^\varepsilon)v+\mu u.\end{cases}$$

Denote by $\Phi^\varepsilon(s,x) := \begin{pmatrix}\bar\varphi(s,x)\\ \bar\psi(s,x)\end{pmatrix}$ the principal eigenvector associated with λ_1^ε (vanishing at $s=\pm a_0$, L periodic in x) normalized by $\|\bar\Phi^\varepsilon\|_{\mathbf{L}^\infty_{per}(\mathbb{R})}=1$, see problem (4.19). Define

$$\begin{aligned}A_0 := \max\big\{A>0 : A\bar\varphi(s,x)\le u(s,x) \text{ and } A\bar\psi(s,x)\le v(s,x),\\ \forall (s,x)\in[-a_0,a_0]\times\mathbb{R}\big\}.\end{aligned}$$

Then we have $A_0\bar\varphi\le u$, $A_0\bar\psi\le v$, with equality at at least one point for at least one equation, say $A_0\bar\varphi(s_0,x_0)=u(s_0,x_0)$ for some $-a_0<s_0<a_0$ and $x_0\in\mathbb{R}$. But

$$L_\varepsilon(u-A_0\bar\varphi)-(r_u-\mu+\lambda_1^\varepsilon)(u-A_0\bar\varphi)\ge \mu(v-A_0\bar\psi)\ge 0,$$

so that the strong maximum principle enforces $u\equiv A_0\bar\varphi$, which is a contradiction since u is positive on $(-a,a)\times\mathbb{R}$ and $\bar\varphi$ vanishes on $\{\pm a_0\}\times\mathbb{R}$. A similar argument leads to a contradiction in the case $v(s_0,x_0)=A_0\bar\psi(s_0,x_0)$. This proves item 5.

Lemma 4.4.3 is proved. □

Item 5 of the above lemma is relevant only when $\lambda_1^\varepsilon<0$, which is actually true if $a_0>0$ is large enough, as proved below. Let us denote by λ_1^ε, $\Phi^\varepsilon(s,x)$

the principal eigenvalue, eigenfunction solving the mixed Dirichlet-periodic eigenproblem

$$\begin{cases} L_\varepsilon \Phi^\varepsilon = A(x)\Phi^\varepsilon + \lambda_1^\varepsilon \Phi^\varepsilon \quad \text{in } \Omega_0 = (-a_0, a_0) \times \mathbb{R} \\ \Phi^\varepsilon(-a_0, x) = \Phi^\varepsilon(a_0, x) = 0 \quad \forall x \in \mathbb{R} \\ \Phi^\varepsilon(s, x) \quad \text{is periodic w.r.t. } x \\ \Phi^\varepsilon > \begin{pmatrix} 0 \\ 0 \end{pmatrix} \text{ in } \Omega_0 = (-a_0, a_0) \times \mathbb{R}. \end{cases} \tag{4.19}$$

Lemma 4.4.4 (An estimate for λ_1^ε). *We have* $\lambda_1^\varepsilon \le \lambda_1 + \frac{5}{2a_0^2}(1+\varepsilon)$.

Proof. Since the matrix $A(x)$ is symmetric, we are equipped with the Rayleigh quotient

$$\lambda_1^\varepsilon = \inf_{\substack{\|w\|_{\mathbf{L}^2}=1 \\ w \in \mathbf{H}^1_{0,per}}} \int_{(-a_0,a_0)\times(0,L)} {}^t w_x w_x + 2\, {}^t w_x w_s + (1+\varepsilon)\, {}^t w_s w_s - {}^t w A(x) w \,\mathrm{d}s\mathrm{d}x.$$

Let us denote $\Phi(x) = \begin{pmatrix} \varphi(x) \\ \psi(x) \end{pmatrix}$ the principal eigenvector solving (4.3), and define

$$\bar\Phi := \|\Phi\|^{-1}_{\mathbf{L}^2_{per}} \Phi.$$

We define the test function $w(s,x) := \eta(s)\bar\Phi(x)$, with $\eta(s) := \sqrt{\frac{15}{16a_0^5}}(a_0 - s)(a_0+s)$, so that $\int_{(-a_0,a_0)} \eta^2(s)ds = 1$. Noticing that $\int {}^t w_x w_s \mathrm{d}x\mathrm{d}s = 0$, we get

$$\lambda_1^\varepsilon \le \int_{(0,L)} ({}^t\bar\Phi_x \bar\Phi_x - {}^t\bar\Phi A(x)\bar\Phi)(x)\mathrm{d}x + \int_{(-a_0,a_0)} (1+\varepsilon)\eta_s^2(s)\mathrm{d}s = \lambda_1 + \frac{5}{2a_0^2}(1+\varepsilon),$$

which shows the result. □

Remark 4.4.5 (Consistency of the choice of parameters in Theorem 4.4.1). Let us say a word on the choice of the positive parameters (a_0^*, ν_0, K_0) in Theorem 4.4.1. First, the choice of a_0^* and Lemma 4.4.4 imply that $\lambda_1^\varepsilon \le \frac{3\lambda_1}{4}$ for any $\varepsilon \in (0,1)$ and $a_0 \ge a_0^*$. Then, (4.18) and the choices of K_0, ν_0 imply that, for $c = 0$,

$$\sup_{\Omega_0} (u+v) \ge \frac{-\lambda_1}{2\gamma^\infty} \ge 2\nu_0.$$

In particular, item 5 in Lemma 4.4.3 gives a true lower bound for $\sup_{\Omega_0} (u+v)$ in the case $c = 0$.

4.4.2 Estimates for the end-point $\tau = 0$ of the first homotopy

We introduce the problem

$$\begin{cases} L_\varepsilon u - cu_s &= u(r_u - \gamma_u(u + \frac{q}{K})) + \mu v - \mu u \\ L_\varepsilon v - cv_s &= v(r_v - \gamma_v(\frac{p}{K} + v)) + \mu u - \mu v \\ (u,v)(-a,x) = (Kp(x), Kq(x)), & \forall x \in \mathbb{R} \\ (u,v)(a,x) = (0,0), & \forall x \in \mathbb{R}, \end{cases} \tag{4.20}$$

which corresponds to (4.17) with $\tau = 0$ and for which comparison methods are available. In this subsection we derive refined estimates for (4.20) that will allow us to enlarge the domain on which the degree is computed, which is necessary for the second homotopy that we will perform.

Lemma 4.4.6 (On problem (4.20))**.** *1. For each $c \in \mathbb{R}$, there exists a unique nonnegative solution (u,v) to* (4.20)*, which satisfies*

$$\forall (s,x) \in \Omega, \quad 0 < u(s,x) < Kp(x) \text{ and } 0 < v(s,x) < Kq(x). \tag{4.21}$$

2. Let $c \in \mathbb{R}$ and (u,v) the nonnegative solution to (4.20)*. Then u and v are nonincreasing in s.*

3. The mapping $c \mapsto \begin{pmatrix} u \\ v \end{pmatrix}$ is decreasing, where (u,v) is the unique nonnegative solution to (4.20)*.*

Proof. In this proof we denote

$$f : \left(x, \begin{pmatrix} u \\ v \end{pmatrix}\right) \mapsto \begin{pmatrix} u(r_u(x) - \gamma_u(x)(u + \frac{q}{K})) + \mu(x)v - \mu(x)u \\ v(r_v(x) - \gamma_v(x)(\frac{p}{K} + v)) + \mu(x)u - \mu(x)v \end{pmatrix} \tag{4.22}$$

so that (4.20) is recast $L_\varepsilon \begin{pmatrix} u \\ v \end{pmatrix} - c \begin{pmatrix} u \\ v \end{pmatrix}_s = f\left(x, \begin{pmatrix} u \\ v \end{pmatrix}\right)$. We select $M > 0$ large enough so that $f(x,\cdot) + MId$ is uniformly nondecreasing on $[0,C]^2$, with C the constant from Lemma 4.4.3, that is

$$\begin{pmatrix} 0 \\ 0 \end{pmatrix} \le \begin{pmatrix} u_1 \\ v_1 \end{pmatrix} \le \begin{pmatrix} u_2 \\ v_2 \end{pmatrix} \le \begin{pmatrix} C \\ C \end{pmatrix}$$
$$\Rightarrow f\left(x, \begin{pmatrix} u_2 \\ v_2 \end{pmatrix}\right) - f\left(x, \begin{pmatrix} u_1 \\ v_1 \end{pmatrix}\right) \ge -M \begin{pmatrix} u_2 - u_1 \\ v_2 - v_1 \end{pmatrix},$$

for all $x \in \mathbb{R}$.

1. We first claim that $(s,x) \mapsto (Kp(x), Kq(x))$ is a strict supersolution to problem (4.20). Since $K \ge K_0$, we have $p + q < Kp \le Kp + \frac{q}{K}$ so

that

$$L_\varepsilon(Kp)-c(Kp)_s=-(Kp)''=(Kp)(r_u(x)-\gamma_u(x)(p+q))+\mu(x)Kq$$
$$-\mu(x)Kp>(Kp)(r_u(x)-\gamma_u(x)(Kp+\frac{q}{K}))+\mu(x)(Kq)-\mu(x)(Kp),$$

and similarly

$$L_\varepsilon(Kq)-c(Kq)_s>(Kq)(r_v(x)-\gamma_v(x)(\frac{p}{K}+Kq))+\mu(x)(Kp)$$
$$-\mu(x)(Kq),$$

which proves the claim. Obviously, $(s,x)\mapsto\begin{pmatrix}0\\0\end{pmatrix}$ is a strict subsolution to problem (4.20) because of the boundary condition at $s=-a$. Since system (4.20) is cooperative, the classical monotone iteration method shows that, for any $c\in\mathbb{R}$, there exists at least a solution (u,v) to problem (4.20) which satisfies (4.21).

Next, in order to prove uniqueness, let (u,v) and $(\tilde u,\tilde v)$ be two non-negative solutions to (4.20), such that $(u,v)\neq(\tilde u,\tilde v)$. Then, for any $0<\zeta<1$, $(U^\zeta,V^\zeta):=(\zeta u,\zeta v)$ satisfies

$$\begin{cases} L_\varepsilon U^\zeta-cU^\zeta_s &= U^\zeta(r_u-\gamma_u\frac{q}{K}-\mu-\frac{\gamma_u(x)}{\zeta}U^\zeta)+\mu(x)V^\zeta\\ &< U^\zeta(r_u-\gamma_u\frac{q}{K}-\mu-\gamma_u(x)U^\zeta)+\mu(x)V^\zeta\\ L_\varepsilon V^\zeta-cV^\zeta_s &= V^\zeta(r_v-\gamma_v\frac{p}{K}-\mu-\frac{\gamma_v(x)}{\zeta}V^\zeta)+\mu(x)U^\zeta\\ &< V^\zeta(r_v-\gamma_v\frac{p}{K}-\mu-\gamma_v(x)V^\zeta)+\mu(x)U^\zeta\\ (U^\zeta,V^\zeta)(-a,x)=(\zeta Kp(x),\zeta Kq(x))\le(Kp(x),Kq(x)) & \\ (U^\zeta,V^\zeta)(a,x)=(0,0), & \end{cases}$$

and is therefore a strict subsolution to problem (4.20). From Hopf lemma we know that $(\tilde u_s,\tilde v_s)(a,x)<(0,0)$ so that we can define

$$\zeta_0:=\sup\{\zeta>0:(U^\zeta,V^\zeta)(s,x)<(\tilde u,\tilde v)(s,x),\forall(s,x)\in\Omega\}>0.$$

Then we have $(0,0)\le(U^{\zeta_0},V^{\zeta_0})\le(\tilde u,\tilde v)\le(C,C)$. Assume by contradiction that $\zeta_0<1$. Then we have

$$\begin{cases} L_\varepsilon(\tilde u-U^{\zeta_0})-c(\tilde u-U^{\zeta_0})_s+M(\tilde u-U^{\zeta_0}) &\ge 0\\ L_\varepsilon(\tilde v-V^{\zeta_0})-c(\tilde v-V^{\zeta_0})_s+M(\tilde v-V^{\zeta_0}) &\ge 0\\ (\tilde u-U^{\zeta_0},\tilde v-V^{\zeta_0})(-a,x)\ge(0,0) & \\ (\tilde u-U^{\zeta_0},\tilde v-V^{\zeta_0})(a,x)=(0,0). & \end{cases}$$

From Hopf lemma we deduce

$$((\tilde u-U^{\zeta_0})_s,(\tilde v-V^{\zeta_0})_s)(a,x)<(0,0)$$

so that there exists $(s_0, x_0) \in (-a, a) \times \mathbb{R}$ such that, say, $\tilde{u}(s_0, x_0) = U^{\zeta_0}(s_0, x_0)$. From the strong maximum principle we deduce $\tilde{u} \equiv U^{\zeta_0}$, which is a contradiction in view of the boundary condition at $s = -a$. We conclude that $\zeta_0 \geq 1$ and thus $(u, v) \leq (\tilde{u}, \tilde{v})$. Then exchanging the roles of (u, v) and $(\tilde{u}, \tilde{v})$ in the above argument, we get that $(\tilde{u}, \tilde{v}) \leq (u, v)$ so that finally $(\tilde{u}, \tilde{v}) = (u, v)$. This is in contradiction with our initial hypothesis. We conclude that the nonnegative solution to equation (4.20) is unique.

2. For given $c \in \mathbb{R}$, let (u, v) be the solution to (4.20). In order to use a sliding technique, we define

$$(u^t(s, x), v^t(s, x)) := (u(s + t, x), v(s + t, x))$$

for $t > 0$ and $(s, x) \in [-a, a - t] \times \mathbb{R}$. From the boundary conditions, there is $\delta > 0$ such that

$$\forall t \in (2a - \delta, 2a), \forall (s, x) \in (-a, a - t) \times \mathbb{R}, \quad u^t(s, x) < u(s, x) \\ \text{and } v^t(s, x) < v(s, x).$$

In particular, one can define

$$t_0 := \inf\{t > 0, \forall (s, x) \in [-a, a - t],\ u^t(s, x) \leq u(s, x) \\ \text{and } v^t(s, x) \leq v(s, x)\}.$$

Assume by contradiction that $t_0 > 0$. Then there exists $(s_0, x_0) \in (-a, a - t_0) \times \mathbb{R}$ such that, say, $u^{t_0}(s_0, x_0) = u(s_0, x_0)$ (notice that $s_0 = -a$ and $s_0 = a - t_0$ are prevented by (4.21)). Since we have

$$L_\varepsilon \begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix} - c \begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix}_s + M \begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix} \\ = (f + M) \begin{pmatrix} u^{t_0} \\ v^{t_0} \end{pmatrix} - (f + M) \begin{pmatrix} u \\ v \end{pmatrix} \leq 0,$$

and $\begin{pmatrix} u^{t_0} - u \\ v^{t_0} - v \end{pmatrix} \leq 0$, the strong maximum principle implies $u^{t_0} \equiv u$, which contradicts $0 < u < Kp$. We conclude that $t_0 = 0$, which means that u and v are nonincreasing in s.

3. Let (c, u, v) and $(\tilde{c}, \tilde{u}, \tilde{v})$ two solutions of equation (4.20) with $c < \tilde{c}$. As above, we define

$$(\tilde{u}^t(s, x), \tilde{v}^t(s, x)) := (\tilde{u}(s + t, x), \tilde{v}(s + t, x)),$$

and

$$t_0 := \inf\{t > 0, \forall (s, x) \in [-a, a - t],\ \tilde{u}^t(s, x) \leq u(s, x) \\ \text{and } \tilde{v}^t(s, x) \leq v(s, x)\}.$$

Assume by contradiction that $t_0 > 0$. Then there again exists $(s_0, x_0) \in (-a, a - t_0) \times \mathbb{R}$ such that, say, $\tilde{u}^{t_0}(s_0, x_0) = u(s_0, x_0)$. Moreover we have

$$L_\varepsilon \begin{pmatrix} \tilde{u}^{t_0} - u \\ \tilde{v}^{t_0} - v \end{pmatrix} - c \begin{pmatrix} \tilde{u}^{t_0} - u \\ \tilde{v}^{t_0} - v \end{pmatrix}_s + M \begin{pmatrix} \tilde{u}^{t_0} - u \\ \tilde{v}^{t_0} - v \end{pmatrix}$$
$$= (f + M) \begin{pmatrix} \tilde{u}^{t_0} \\ \tilde{v}^{t_0} \end{pmatrix} - (f + M) \begin{pmatrix} u \\ v \end{pmatrix} + (\tilde{c} - c) \begin{pmatrix} \tilde{u}^{t_0} \\ \tilde{v}^{t_0} \end{pmatrix}_s$$
$$\leq \begin{pmatrix} 0 \\ 0 \end{pmatrix},$$

since $\tilde{u}_s \leq 0$ and $\tilde{v}_s \leq 0$ (recall that $\tilde{u}$ and $\tilde{v}$ are decreasing), so that we again derive a contradiction. As a result $t_0 = 0$, that is $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \leq \begin{pmatrix} u \\ v \end{pmatrix}$ and then $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} < \begin{pmatrix} u \\ v \end{pmatrix}$ from the strong maximum principle.

The lemma is proved. □

4.4.3 Estimates along the second homotopy

The second homotopy allows us to get rid of the nonlinearity and the coupling in u and v at the expense of an increased linear part. For $0 \leq \tau \leq 1$, we consider

$$\begin{cases} L_\varepsilon u - c u_s = \tau \left(u \left(r_u - \gamma_u \frac{q}{K} - \mu - \gamma_u u \right) + \mu v \right) - (1 - \tau) \mathcal{C} u \\ L_\varepsilon v - c v_s = \tau \left(v \left(r_v - \gamma_v \frac{p}{K} - \mu - \gamma_v v \right) + \mu u \right) - (1 - \tau) \mathcal{C} v \\ (u, v)(-a, x) = (K p(x), K q(x)), \quad \forall x \in \mathbb{R} \\ (u, v)(a, x) = (0, 0), \quad \forall x \in \mathbb{R}, \end{cases} \tag{4.23}$$

with

$$\mathcal{C} := -\min_{x \in \mathbb{R}} \Bigg(r_u(x) - \gamma_u(x) \left(\frac{q(x)}{K} + C \right) - \mu(x), \\ r_v(x) - \gamma_v(x) \left(\frac{p(x)}{K} + C \right) - \mu(x), 0 \Bigg), \tag{4.24}$$

where C is as in Lemma 4.4.3 item 2.

Lemma 4.4.7 (A priori estimates along the second homotopy). *Let a nonnegative $(u, v) \in \mathbf{C}^1_{per}(\Omega)$ (where $\Omega = (-a, a) \times \mathbb{R}$ and the periodicity is understood only w.r.t. the $x \in \mathbb{R}$ variable) and $c \in \mathbb{R}$ solve* (4.23)*, with $0 \leq \tau \leq 1$. Then*

1. *(u, v) is a classical solution to* (4.23)*, i.e. $(u, v) \in \mathbf{C}^2(\overline{\Omega})$.*

2. *We have*

$$u(s,x)+v(s,x)\le C, \quad \forall (s,x)\in\bar\Omega=[-a,a]\times\mathbb{R}.$$

3. (u,v) *is positive in* Ω.

4. *If* $a\ge a_0+\bar a$ *and* $c\ge \bar c^{\varepsilon}$, *we have* $\sup\limits_{\Omega_0}(u+v)<\frac{\nu}{2}$, *where* $\bar a$ *is as in Lemma 4.4.3 item 4.*

5. *There exists* $\underline{c}=\underline{c}(a)\ge 0$ *such that if* $c\le -\underline{c}(a)$ *then* $\sup\limits_{\Omega_0}(u+v)>\nu$.

Proof. Items 1, 2, 3 and 4 can be proved as in Lemma 4.4.3. We therefore omit the details, and only focus on item 5.

From item 2 and the choice of $\mathcal{C}$ we see that, for any $0\le\tau\le 1$,

$$L_\varepsilon u - cu_s+\mathcal{C}u\ge 0, \quad u(-a,x)=Kp(x), \quad u(a,x)=0.$$

Now, let $\alpha_\pm := \frac{-c\pm\sqrt{c^2+4(1+\varepsilon)\mathcal{C}}}{2(1+\varepsilon)}$ and $m:=K\min\limits_{x\in\mathbb{R}}(p(x),q(x))>0$. Then the function $\theta(s,x)=\theta(s):=m\frac{e^{\alpha_- s+\alpha_+ a}-e^{\alpha_+ s+\alpha_- a}}{e^{(\alpha_+-\alpha_-)a}-e^{(\alpha_--\alpha_+)a}}$ solves

$$L_\varepsilon\theta - c\theta_s+\mathcal{C}\theta=0, \quad \theta(-a)=m, \quad \theta(a)=0.$$

From the comparison principle, we infer that $u(s,x)\ge\theta(s)$, and similarly $v(s,x)\ge\theta(s)$, for all $(s,x)\in(-a,a)\times\mathbb{R}$. As a result $\sup\limits_{\Omega_0}(u+v)\ge 2\sup_{(-a_0,a_0)}\theta\ge 2\theta(0)$.

Next, for $c\le -c^1(a):=-\frac{1+\varepsilon}{a}\ln 4$ one has $e^{(\alpha_--\alpha_+)a}\le\frac14$ so that

$$\theta(0)\ge m\frac{e^{\alpha_+ a}-e^{\alpha_- a}}{e^{(\alpha_+-\alpha_-)a}}=me^{\alpha_- a}\left(1-e^{(\alpha_--\alpha_+)a}\right)\ge m\frac{3e^{\alpha_- a}}{4}.$$

Next, thanks to a Taylor expansion, we have

$$\begin{aligned}\alpha_- &= \frac{-c}{2(1+\varepsilon)}\left(1-\sqrt{1+\frac{4(1+\varepsilon)\mathcal{C}}{c^2}}\right)\\ &\qquad\qquad = \frac{-c}{2(1+\varepsilon)}\left(-\frac{2(1+\varepsilon)\mathcal{C}}{c^2}+o\left(\frac{1}{c^2}\right)\right)=\frac{\mathcal{C}}{c}+o\left(\frac{1}{|c|}\right)\end{aligned}$$

so that there exists $c^2=c^2(a)>0$ such that for any $c\le -c^2(a)$ we have $e^{\alpha_- a}>\frac23$. As a result when $c\le-\underline{c}(a):=-\max(c^1(a),c^2(a))$, we have

$$\sup_{\Omega_0}(u+v)\ge m\ge\nu_0>\nu,$$

which proves item 5. □

4.4.4 Proof of Theorem 4.4.1

Equipped with the above estimates, we are now in the position to prove Theorem 4.4.1 using three homotopies and the Leray Schauder topological degree. To do so, let us define the following open subset of $\mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$

$$\Gamma := \left\{ \left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) \in \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) : c \in (0, \overline{c}^{\varepsilon} + \varepsilon), \begin{pmatrix} 0 \\ 0 \end{pmatrix} < \begin{pmatrix} u \\ v \end{pmatrix} < \begin{pmatrix} C \\ C \end{pmatrix} \text{ in } \Omega \right\}$$

where $\Omega = (-a, a) \times \mathbb{R}$, and $C > 0$ is the constant defined in Lemma 4.4.3 item 2.

• We develop the first homotopy argument. For $0 \leq \tau \leq 1$, let us define the operator

$$F_\tau : \quad \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) \quad \to \quad \mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$$

where $F_\tau \left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) = \left(\tilde{c}, \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix} \right)$, with

$$\tilde{c} = c + \sup_{\Omega_0} (\tilde{u} + \tilde{v}) - \nu$$

and $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}$ is the unique solution in $\mathbf{C}^1_{per}(\Omega)$ of the linear problem

$$\begin{cases} L_\varepsilon \tilde{u} - c\tilde{u}_s &= u(r_u - \gamma_u(u + (\tau v + (1-\tau)\frac{q}{K}))) + \mu v - \mu u \\ L_\varepsilon \tilde{v} - c\tilde{v}_s &= v(r_v - \gamma_v((\tau u + (1-\tau)\frac{p}{K}) + v)) + \mu u - \mu v \\ (u, v)(-a, x) = (Kp(x), Kq(x)), & \forall x \in \mathbb{R} \\ (u, v)(a, x) = (0, 0), & \forall x \in \mathbb{R}. \end{cases}$$

From standard elliptic estimates, for any $0 \leq \tau \leq 1$, F_τ maps $\mathbf{C}^1_{per}(\Omega)$ into $\mathbf{C}^2_{per}(\overline{\Omega})$, which shows that F_τ is a compact operator in $\mathbf{C}^1_{per}(\Omega)$. Moreover F_τ depends continuously on the parameter $0 \leq \tau \leq 1$. The Leray-Schauder topological argument can thus be applied: in order to prove that the degree is independent of the parameter τ, it suffices to show that there is no fixed point of F_τ on the boundary $\partial\Gamma$, which will be a consequence of estimates in subsection 4.4.1. Indeed, let $\left(c, \begin{pmatrix} u \\ v \end{pmatrix} \right) = (c, u, v)$ be a fixed point of F_τ in $\overline{\Gamma}$.

1. From Lemma 4.4.3, Lemma 4.4.4 and Remark 4.4.5 we know that if $c = 0$ then $\sup_{\Omega_0} (u + v) > \nu$ so that $\tilde{c} > c$, which is absurd. That shows $c \neq 0$.

2. From Lemma 4.4.3 we know that if $c \geq \overline{c}^{\varepsilon}$ then $\sup_{\Omega_0} (u + v) < \nu$ so that $\tilde{c} < c$, which is absurd. That shows $c < \overline{c}^{\varepsilon} + \varepsilon$.

3. From Lemma 4.4.3 we know that $u < C$ and $v < C$.
4. From Lemma 4.4.3 and the boundary condition at $s = -a$, we know that $u > 0$ and $v > 0$ in $[-a, a) \times \mathbb{R}$. Moreover, we know from Hopf lemma that $\forall x \in \mathbb{R}$, $u_s(a, x) < 0$ and $v_s(a, x) < 0$.

As a result, $(c, u, v) \notin \partial\Gamma$ so that

$$\deg(Id - F_1, \Gamma, 0) = \deg(Id - F_0, \Gamma, 0). \tag{4.25}$$

• We now consider the second homotopy. For $0 \le \tau \le 1$, let us define the operator

$$\begin{array}{rccc} G_\tau : & \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) & \to & \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) \\ & \left(c, \begin{pmatrix} u \\ v \end{pmatrix}\right) & \mapsto & \left(\tilde{c}, \begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}\right) \end{array}$$

with again

$$\tilde{c} = c + \sup_{\Omega_0} (\tilde{u} + \tilde{v}) - \nu$$

and $\begin{pmatrix} \tilde{u} \\ \tilde{v} \end{pmatrix}$ is the unique solutions in $\mathbf{C}^1_{per}(\Omega)$ of the linear problem

$$\begin{cases} L_\varepsilon \tilde{u} - c\tilde{u}_s + (1-\tau)\mathcal{C}\tilde{u} = \tau \left(u \left(r_u - \gamma_u \frac{q}{K} - \mu - \gamma_u u\right) + \mu v\right) \\ L_\varepsilon \tilde{v} - c\tilde{v}_s + (1-\tau)\mathcal{C}\tilde{v} = \tau \left(v \left(r_v - \gamma_v \frac{p}{K} - \mu - \gamma_v v\right) + \mu u\right) \\ (u, v)(-a, x) = (Kp(x), Kq(x)), \quad \forall x \in \mathbb{R} \\ (u, v)(a, x) = (0, 0), \quad \forall x \in \mathbb{R}, \end{cases}$$

and $\mathcal{C}$ is defined by (4.24). Notice that G_τ is a continuous family of compact operators and that $G_1 = F_0$. From Lemma 4.4.3 and Lemma 4.4.6, we see that there is no fixed point of F_0 such that $c \le 0$ since $c \mapsto \begin{pmatrix} u \\ v \end{pmatrix}$ is nonincreasing. As a result, enlarging Γ into

$$\tilde{\Gamma} := \left\{ \left(c, \begin{pmatrix} u \\ v \end{pmatrix}\right) \in \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) : c \in (-\underline{c}(a), \bar{c}^\varepsilon + \varepsilon), \right.$$
$$\left. \begin{pmatrix} 0 \\ 0 \end{pmatrix} < \begin{pmatrix} u \\ v \end{pmatrix} < \begin{pmatrix} C \\ C \end{pmatrix} \text{ in } \Omega \right\},$$

with $\underline{c}(a) \ge 0$ as in Lemma 4.4.7, does not alter the degree, that is

$$\deg(Id - F_0, \Gamma, 0) = \deg(Id - F_0, \tilde{\Gamma}, 0) = \deg(Id - G_1, \tilde{\Gamma}, 0). \tag{4.26}$$

Next, using the estimates of Lemma 4.4.7 and Hopf lemma as above, we see that there is no fixed point of G_τ on the boundary $\partial\tilde{\Gamma}$. We have then

$$\deg(Id - G_1, \tilde{\Gamma}, 0) = \deg(Id - G_0, \tilde{\Gamma}, 0). \tag{4.27}$$

Now G_0 is independent of (u,v). Since $L_\varepsilon - c\partial_s + \mathcal{C}Id$ is invertible for each $c \in \mathbb{R}$, there exists exactly one solution of (4.23) with $\tau = 0$ for each $c \in \mathbb{R}$, which we denote (u_c, v_c). Thanks to a sliding argument, which we omit here, the solutions to (4.23) with $\tau = 0$ are nonincreasing in s and $c \mapsto (u_c, v_c)$ is decreasing, so that there exists a unique $c \in (-\underline{c}(a), \overline{c}^\varepsilon + \varepsilon)$, which we denote c_0, such that (c_0, u_{c_0}, v_{c_0}) is a fixed point to G_0.

• Finally a third homotopy allows us to compute the degree. For $0 \leq \tau \leq 1$, let us define the operator $H_\tau : \mathbb{R} \times \mathbf{C}^1_{per}(\Omega) \to \mathbb{R} \times \mathbf{C}^1_{per}(\Omega)$ by

$$H_\tau(c,u,v) = \left(c + \sup_{\Omega_0} (u_c + v_c) - \nu, \tau u_c + (1-\tau) u_{c_0}, \tau v_c + (1-\tau) v_{c_0} \right).$$

Noticing that $H_1 = G_0$ and that, again, H_τ has no fixed point on the boundary $\partial\tilde{\Gamma}$, we obtain

$$\deg(Id - G_0, \tilde{\Gamma}, 0) = \deg(Id - H_1, \tilde{\Gamma}, 0) = \deg(Id - H_0, \tilde{\Gamma}, 0). \tag{4.28}$$

Then since H_0 has separated variables and $c \mapsto \sup_{\Omega_0} (u_c + v_c)$ is decreasing, we see that

$$\deg(Id - H_0, \tilde{\Gamma}, 0) = 1. \tag{4.29}$$

• Combining (4.25), (4.26), (4.27), (4.28) and (4.29), we get $\deg(Id - F_1, \Gamma, 0) = 1$, which shows the existence of a solution to (4.15) in $\mathbf{C}^1_{per}(\Omega)$. Theorem 4.4.1 is proved. $\square$

4.5 Pulsating fronts

From the previous section, we are equipped with a solution to (4.15) in the strip $(-a,a) \times \mathbb{R}$. From the estimates of Theorem 4.4.1 and standard elliptic estimates, we can — up to a subsequence— let $a \to \infty$ and then recover, for any $0 < \varepsilon < 1$, a speed $0 < c = c^\varepsilon < \overline{c}^\varepsilon + \varepsilon$ and smooth profiles $(0,0) < (u(s,x), v(s,x)) = (u^\varepsilon(s,x), v^\varepsilon(s,x)) < (C,C)$ solving

$$\begin{cases} -u_{xx} - 2u_{xs} - (1+\varepsilon)u_{ss} - cu_s = u(r_u - \gamma_u(u+v)) + \mu v - \mu u & \text{in } \mathbb{R}^2 \\ -v_{xx} - 2v_{xs} - (1+\varepsilon)v_{ss} - cv_s = v(r_v - \gamma_v(u+v)) + \mu u - \mu v & \text{in } \mathbb{R}^2 \\ (u,v)(s,\cdot) \quad \text{is } L\text{-periodic} \\ \sup_{\Omega_0} (u+v) = \nu. \end{cases} \tag{4.30}$$

Let us mention again that, because of the lack of comparison, we do not know that the above solution is decreasing in s, in sharp contrast with the previous results on pulsating fronts [203, 18, 133, 20, 120, 126]. To overcome this lack of monotony, further estimates will be required.

Now, the main difficulty is to show that, letting $\varepsilon \to 0$, we recover a nonzero speed and thus a pulsating front. To do so, it is not convenient to use the (s, x) variables, and we therefore switch to functions

$$\tilde{u}(t,x) := u(x-ct, x), \quad \tilde{v}(t,x) := v(x-ct, x), \quad (t,x) \in \mathbb{R}^2,$$

which are consistent with Definition 4.2.5 of a pulsating front. Hence, after dropping the tildes, (4.30) is recast

$$\begin{cases} -\frac{\varepsilon}{c^2} u_{tt} - u_{xx} + u_t &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \quad \text{in } \mathbb{R}^2 \\ -\frac{\varepsilon}{c^2} v_{tt} - v_{xx} + v_t &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v \quad \text{in } \mathbb{R}^2 \\ \sup\limits_{x-ct \in (-a_0, a_0)} u(t,x) + v(t,x) = \nu. \end{cases} \tag{4.31}$$

Also the L periodicity for (4.30) is transferred into the constraint (4.6) for (4.31). Moreover, up to a translation, we can assume w.l.o.g. that the solution to (4.31) satisfies

$$\sup_{x \in (-a_0, a_0)} (u(0,x) + v(0,x)) = \nu. \tag{4.32}$$

Also, though t can be interpreted as a time, we would like to stress out that (4.31) is not a Cauchy problem.

Our first goal in this section is to let $\varepsilon \to 0$ in (4.31) and get the following.

Theorem 4.5.1 (Letting the regularization tend to zero)**.** *There exist a speed $0 < c \leq \bar{c}^0 := \lim_{\varepsilon \to 0} \bar{c}^\varepsilon$ (see Lemma 4.4.2) and positive profiles (u, v) solving, in the classical sense,*

$$\begin{cases} u_t - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu(v-u) \quad \text{in } \mathbb{R}^2 \\ v_t - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu(u-v) \quad \text{in } \mathbb{R}^2, \end{cases} \tag{4.33}$$

satisfying the constraint (4.6) *and, for some $a_0 > 0$, the normalization*

$$\sup_{x-ct \in (-a_0, a_0)} (u+v) = \nu.$$

The present section is organized as follows. After proving further estimates on solutions to (4.31) in subsection 4.5.1, we prove Theorem 4.5.1 in subsection 4.5.2, the main difficulty being to exclude the possibility of a standing wave. Finally, in subsection 4.5.3 we conclude the construction of a pulsating front, thus proving our main result Theorem 4.2.6.

4.5.1 Lower estimates on solutions to (4.31)

We start by showing a uniform lower bound on the solutions to (4.31) that have a positive lower bound. The argument relies on the sign of the eigenvalue λ_1, or more precisely that of the first eigenvalue to the stationary

Dirichlet problem in large bouded domains. For $b>0$, we denote (λ_1^b, Φ^b) with $\Phi^b(x) := \begin{pmatrix}\varphi^b(x)\\ \psi^b(x)\end{pmatrix}$ the unique eigenpair solving

$$\begin{cases} -\Phi^b_{xx} - A(x)\Phi^b = \lambda_1^b \Phi^b \\ \varphi^b(x) > 0,\ \psi^b(x) > 0, \quad x \in (-b,b) \\ \varphi^b(\pm b) = \psi^b(\pm b) = 0, \end{cases} \tag{4.34}$$

and $\|\Phi^b\|_{\mathbf{L}^\infty(-b,b)} = 1$. From Lemma 4.6.5, we know that $\lambda_1^b \to \lambda_1 < 0$ when $b \to \infty$. We can thus select $a_1 > a_0^*$, with a_0^* as in Theorem 4.4.1, large enough so that

$$b \geq a_1 \Rightarrow \lambda_1^b \leq \frac{3\lambda_1}{4}. \tag{4.35}$$

Also, from Hopf lemma we have $C^b := \sup\limits_{x\in(-b,b)} \left(\frac{\varphi^b(x)}{\psi^b(x)}, \frac{\psi^b(x)}{\varphi^b(x)}\right) < +\infty$.

Lemma 4.5.2 (A uniform lower estimate). *Let $(u(t,x), v(t,x))$ be a classical positive solution to*

$$\begin{cases} \beta u_t - \kappa u_{tt} - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \quad \text{in } \mathbb{R}^2 \\ \beta v_t - \kappa v_{tt} - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v \quad \text{in } \mathbb{R}^2, \end{cases} \tag{4.36}$$

with $\kappa \geq 0$ and $\beta \in \mathbb{R}$. Let also $b \geq a_1$ and Φ^b the solution to (4.34).

Then there exists a constant $\alpha_0 = \alpha_0(\mu^0, \gamma^\infty, \lambda_1^b, C^b) > 0$ such that if

$$\inf_{(t,x)\in\mathbb{R}\times(-b,b)} \min(u(t,x), v(t,x)) > 0$$

then

$$\forall (t,x) \in \mathbb{R}\times(-b,b),\ \begin{pmatrix}u(t,x)\\ v(t,x)\end{pmatrix} \geq \alpha_0 \Phi^b(x).$$

Proof. Let $0 < \eta \leq 1$ be given. For $\alpha > 0$, we define

$$\begin{pmatrix}U^{\alpha,\eta}(t,x)\\ V^{\alpha,\eta}(t,x)\end{pmatrix} := \alpha(1-\eta t^2)\begin{pmatrix}\varphi^b(x)\\ \psi^b(x)\end{pmatrix}.$$

Then for small $\alpha < \min\left(\inf\limits_{(t,x)\in\mathbb{R}\times(-b,b)} u, \inf\limits_{(t,x)\in\mathbb{R}\times(-b,b)} v\right)$ we have the inequality $\begin{pmatrix}U^{\alpha,\eta}(t,x)\\ V^{\alpha,\eta}(t,x)\end{pmatrix} \leq \begin{pmatrix}u(t,x)\\ v(t,x)\end{pmatrix}$ for all $(t,x) \in \mathbb{R}\times(-b,b)$, whereas for large $\alpha > \frac{\max(u(0,0),v(0,0))}{\min(\varphi^b(0),\psi^b(0))}$ one has $\begin{pmatrix}U^{\alpha,\eta}(0,0)\\ V^{\alpha,\eta}(0,0)\end{pmatrix} > \begin{pmatrix}u(0,0)\\ v(0,0)\end{pmatrix}$. Thus we can define

$$\alpha_0^\eta = \alpha_0 := \sup\left\{\alpha > 0, \forall (t,x) \in \mathbb{R}\times(-b,b), \begin{pmatrix}U^{\alpha,\eta}(t,x)\\ V^{\alpha,\eta}(t,x)\end{pmatrix} \leq \begin{pmatrix}u(t,x)\\ v(t,x)\end{pmatrix}\right\} > 0.$$

Assume by contradiction that

$$\alpha_0 \leq \alpha_0^* := \min\left(1, \frac{\mu^0}{2\gamma^\infty}, \frac{-\lambda_1^b}{2(1+2C^b)\gamma^\infty}\right).$$

There exists a touching point $(t_0, x_0) \in (-\sqrt{\eta}, \sqrt{\eta}) \times (-b, b)$ such that either $u(t_0, x_0) = U^{\alpha_0,\eta}(t_0, x_0)$ or $v(t_0, x_0) = V^{\alpha_0,\eta}(t_0, x_0)$. Assume $u(t_0, x_0) = U^{\alpha_0,\eta}(t_0, x_0)$ for instance. Then $u - U^{\alpha_0,\eta}$ reaches a zero minimum at (t_0, x_0) so that

$$\begin{aligned} 0 &\geq \beta\left(u - U^{\alpha_0,\eta}\right)_t - \kappa\left(u - U^{\alpha_0,\eta}\right)_{tt} - \left(u - U^{\alpha_0,\eta}\right)_{xx} \\ &= (\beta u_t - \kappa u_{tt} - u_{xx}) + \alpha_0(1-\eta t_0^2)\varphi^b_{xx} + 2\alpha_0\beta\eta t_0\varphi^b - 2\alpha_0\kappa\eta\varphi^b \end{aligned}$$

at point (t_0, x_0). Using (4.34) and (4.36) yields

$$\begin{aligned} 0 \geq u(r_u - \mu - \gamma_u(u+v)) + \mu v - \alpha_0(1-\eta t_0^2)(\varphi^b(r_u - \mu + \lambda_1^b) + \mu\psi^b) \\ + 2\alpha_0\eta\varphi^b(\beta t_0 - \kappa) \end{aligned}$$

at point (t_0, x_0), and since $u(t_0, x_0) = \alpha_0(1 - \eta t_0^2)\varphi^b(x_0)$ we end up with

$$\begin{aligned} 0 \geq u_0[-\lambda_1^b - \gamma_u(x_0)(u_0 + v_0)] + \mu(x_0)[v_0 - \alpha_0(1-\eta t_0^2)\psi^b(x_0)] \\ + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa), \end{aligned} \tag{4.37}$$

with the notations $u_0 = u(t_0, x_0)$, $v_0 = v(t_0, x_0)$. Now two cases may occur.

• Assume first that $v_0 \leq 2\alpha_0(1 - \eta t_0^2)\psi^b(x_0)$. Then we have

$$v_0 \leq 2\alpha_0(1-\eta t_0^2)\frac{\psi^b(x_0)}{\varphi^b(x_0)}\varphi^b(x_0) \leq 2C^b u_0,$$

and since $v_0 - \alpha_0(1 - \eta t_0^2)\psi^b(x_0) \geq 0$, we deduce from (4.37) that

$$\gamma_u(x_0)(1+2C^b)u_0^2 \geq -\lambda_1^b u_0 + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa),$$

which in turn implies

$$\begin{aligned} \gamma^\infty(1+2C^b)\alpha_0 \geq \gamma_u(x_0)(1+2C^b)u_0 \geq -\lambda_1^b + \frac{2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa)}{u_0} \\ \geq -\lambda_1^b - \frac{2\eta}{\inf u}(|\beta||t_0| + \kappa), \end{aligned}$$

since $\alpha_0 \leq 1$ and $\varphi^b \leq 1$. Since $|t_0| \leq \frac{1}{\sqrt{\eta}}$, one then has

$$\alpha_0 \geq \frac{-\lambda_1^b}{(1+2C^b)\gamma^\infty} - 2\sqrt{\eta}\frac{|\beta| + \kappa}{(1+2C^b)\gamma^\infty \inf u}. \tag{4.38}$$

• On the other hand, assume $v_0 \geq 2\alpha_0(1-\eta t_0^2)\psi^b(x_0)$. Then we deduce from (4.37) that

$$\begin{aligned}\gamma_u(x_0)u_0^2 \geq & -\lambda_1^b u_0 + \frac{\mu(x_0)}{2}(v_0 - 2\alpha_0(1-\eta t_0^2)\psi^b(x_0)) \\ & + v_0\left(\frac{\mu(x_0)}{2} - \gamma_u(x_0)u_0\right) + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa) \\ \geq & -\lambda_1^b u_0 + 2\alpha_0\eta\varphi^b(x_0)(\beta t_0 - \kappa),\end{aligned}$$

since $\gamma_u u \leq \gamma_u \alpha_0^* \leq \frac{\mu^0}{2}$. Arguing as in the first case, we end up with

$$\alpha_0 \geq \frac{-\lambda_1^b}{\gamma^\infty} - 2\sqrt{\eta}\frac{|\beta|+\kappa}{\gamma^\infty \inf u}. \tag{4.39}$$

From (4.38) , (4.39) and the symmetric situation where $v(t_0,x_0) = V^{\alpha_0,\eta}(t_0,x_0)$, we deduce that, in any case,

$$\alpha_0 \geq \frac{-\lambda_1^b}{(1+2C^b)\gamma^\infty} - 2\sqrt{\eta}\frac{|\beta|+\kappa}{\gamma^\infty \inf(u,v)}. \tag{4.40}$$

One sees that for

$$0 < \eta < \eta^* := \min\left(1, \left(\frac{-\lambda_1^b \inf(u,v)}{4(|\beta|+\kappa)(1+2C^b)}\right)^2\right),$$

inequality (4.40) is a contradiction since it implies $\alpha_0 > \alpha_0^*$. Hence we have shown that for any $0 < \eta < \eta^*$ one has $\alpha_0 = \alpha_0^\eta > \alpha_0^*$. In particular

$$\forall \eta \in (0,\eta^*), \forall (t,x) \in \mathbb{R} \times (-b,b), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha_0^*(1-\eta t^2)\begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix}.$$

Taking the limit $\eta \to 0$, we then obtain

$$\forall (t,x) \in \mathbb{R} \times (-b,b), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha_0^*\Phi^b(x),$$

which concludes the proof of Lemma 4.5.2. □

Next we establish a forward-in-time lower estimate for solutions of the (possibly degenerate) problem (4.41). The proof is based on the same idea as in Lemma 4.5.2, but it is here critical that the coefficient β of the time-derivative has the right sign. Roughly speaking, the following lemma asserts that once a population has reached a certain threshold on a large enough set, it cannot fall under that threshold at a later time.

Lemma 4.5.3 (A forward-in-time lower estimate)**.** *Let $(u(t,x),v(t,x))$ be a classical positive solution to*

$$\begin{cases} \beta u_t - \kappa u_{tt} - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \quad \text{in } \mathbb{R}^2 \\ \beta v_t - \kappa v_{tt} - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v \quad \text{in } \mathbb{R}^2, \end{cases} \tag{4.41}$$

with $\kappa \geq 0$ and $\beta \geq 0$. Let also $b \geq a_1$ and Φ^b the solution to (4.34).

Then there exists a constant $\alpha_0 = \alpha_0(\mu^0, \gamma^\infty, \lambda_1^b, C^b) > 0$ such that if $0 < \alpha < \alpha_0$ and

$$\forall x \in (-b,b),\ \alpha \Phi^b(x) < \begin{pmatrix} u(0,x) \\ v(0,x) \end{pmatrix}, \tag{4.42}$$

then

$$\forall t > 0, \forall x \in (-b,b),\ \alpha \Phi^b(x) \leq \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix}.$$

Proof. Let

$$0 < \alpha < \alpha_0 := \min\left(1, \frac{-\lambda_1^b}{2(1+2C^b)\gamma^\infty}, \frac{\mu^0}{2\gamma^\infty}\right)$$

and assume (4.42). For $\eta > 0$ we define

$$\zeta(t,x) = \begin{pmatrix} \zeta_u(t,x) \\ \zeta_v(t,x) \end{pmatrix} := \alpha(1-\eta t) \begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix}.$$

From (4.42), we can define

$$\eta_0 := \inf\left\{\eta \in \mathbb{R} : \forall t \geq 0, \forall x \in [-b,b], \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \zeta(t,x)\right\}.$$

Assume by contradiction that $\eta_0 > 0$. Then there exists $t_0 > 0$ and $x_0 \in (-b,b)$ such that, say, $u(t_0,x_0) = \zeta_u(t_0,x_0)$. Then at point (t_0,x_0) we have

$$\begin{aligned} 0 \geq \beta(u-\zeta_u)_t - \kappa(u-\zeta_u)_{tt} - (u-\zeta_u)_{xx} = u(r_u - \gamma_u(u+v)) + \mu(v-u) \\ + \zeta_{u_{xx}} + \beta\alpha\eta\varphi^b. \end{aligned}$$

Using (4.34) and $u(t_0,x_0) = \alpha(1-\eta_0 t_0)\varphi^b(x_0)$, we end up with

$$0 \geq u_0(-\lambda_1^b - \gamma_u(x_0)(u_0+v_0)) + \mu(x_0)(v_0 - \zeta_v(t_0,x_0)), \tag{4.43}$$

with the notations $u_0 = u(t_0,x_0)$, $v_0 = v(t_0,x_0)$ and thanks to $\beta \geq 0$. Now two cases may occur.

- Assume first that $v_0 \leq 2\zeta_v(t_0,x_0)$. Then $v_0 \leq 2\frac{\zeta_v(t_0,x_0)}{\zeta_u(t_0,x_0)}\zeta_u(t_0,x_0) \leq 2C^b\zeta_u(t_0,x_0) = 2C^b u_0$, so that (4.43) yields (recall that $v_0 \geq \zeta_v(t_0,x_0)$)

$$\gamma_u(x_0)(1+2C^b)u_0^2 \geq \gamma_u(x_0)(u_0+v_0)u_0 \geq -\lambda_1^b u_0.$$

As a result $u_0 > \alpha_0$, which is a contradiction.

• Assume now that $v_0 \geq 2\zeta_v(t_0, x_0)$. Then we deduce from (4.43) that

$$\begin{aligned}
\gamma_u(x_0)u_0^2 &\geq -\lambda_1^b u_0 + v_0 \left(\frac{\mu(x_0)}{2} - \gamma_u(x_0)u_0\right) + \frac{\mu(x_0)}{2}(v_0 - 2\zeta_v(t_0, x_0)) \\
&\geq -\lambda_1^b u_0 + \frac{1}{2}\mu(x_0)(v_0 - 2\zeta_v(t_0, x_0)),
\end{aligned}$$

since $u_0 \leq \alpha_0 \leq \frac{\mu^0}{2\gamma^\infty}$. As a result $u_0 \geq \frac{-\lambda_1^b}{\gamma^\infty} > \alpha_0$, which is also a contradiction.

Thus $\eta_0 \leq 0$ and in particular

$$\forall t > 0, \forall x \in (-b, b), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha \begin{pmatrix} \varphi^b(x) \\ \psi^b(x) \end{pmatrix},$$

which concludes the proof of Lemma 4.5.3. □

4.5.2 Proof of Theorem 4.5.1

In this subsection, we prove that a well-chosen series of solutions to equation (4.31) cannot converge, as $\varepsilon \to 0$, to a standing wave ($c = 0$). In other words, we prove Theorem 4.5.1, making a straightforward use of the crucial Lemma 4.5.4. The rough idea of the proof of Lemma 4.5.4 is that a standing wave cannot stay in the neighborhood of 0 for a long time. Hence the normalization allows us to prevent a sequence of solutions from converging to a standing wave, provided ν is chosen small enough. Notice also that the interior gradient estimate for elliptic systems of Lemma 4.6.4 will be used.

In the sequel we select $a_1 > a_0^*$ as in (4.35), recall that $\lambda_1^{a_1}$ denotes the eigenvalue of problem (4.34) in the domain $(-a_1, a_1)$, and define

$$\nu^* := \frac{1}{2}\min(\nu_0, \underline{\nu}) > 0,$$

where $\underline{\nu} := \alpha_0 \inf_{x \in (-a_0^*, a_0^*)} \min(\varphi^{a_1}(x), \psi^{a_1}(x))$, with $\alpha_0 > 0$ the constant in Lemma 4.5.2 in the domain $(-a_1, a_1)$.

Lemma 4.5.4 (Nonzero limit speed)**.** *Let* $(\varepsilon_n, c_n, u^n(t,x), v^n(t,x))$ *be a sequence such that* $\varepsilon_n > 0$*,* $\varepsilon_n \to 0$*,* $c_n \neq 0$*,* (u^n, v^n) *is a positive solution to problem* (4.31) *with* $\varepsilon = \varepsilon_n$*,* $c = c_n$*,* $0 < \nu < \nu^*$ *and* $a_0 > a_1$*. Then*

$$\liminf_{n\to\infty} c_n > 0. \tag{4.44}$$

Proof. Assume by contradiction that there is a sequence as in Lemma 4.5.4 with $\lim c_n = 0$. Define the sequence $\kappa_n := \frac{\varepsilon_n}{c_n^2} > 0$ which, up to an extraction, tends to $+\infty$, or to some $\kappa \in (0, +\infty)$ or to 0. In each case we are going to construct a couple of functions (u,v) that shows a contradiction. We refer to [18] or to [20] for a similar trichotomy.

Case 1: $\kappa_n \to +\infty$. Defining $(\tilde{u}^n, \tilde{v}^n)(t,x) := (u^n, v^n)(\sqrt{\kappa_n}t, x)$, problem (4.31) is recast

$$\begin{cases} -u^n_{tt} - u^n_{xx} + \frac{1}{\sqrt{\kappa_n}} u^n_t &= u^n(r_u - \gamma_u(u^n+v^n)) + \mu v^n - \mu u^n \\ -v^n_{tt} - v^n_{xx} + \frac{1}{\sqrt{\kappa_n}} v^n_t &= v^n(r_v - \gamma_v(u^n+v^n)) + \mu u^n - \mu v^n \\ \sup\limits_{x-\sqrt{\varepsilon_n}t \in (-a_0,a_0)} u^n(t,x) + v^n(t,x) = \nu, \end{cases} \tag{4.45}$$

where we have dropped the tildes. From standard elliptic estimates, this sequence converges, up to an extraction, to a classical nonnegative solution (u,v) of

$$\begin{cases} -u_{tt} - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \\ -v_{tt} - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v, \end{cases} \tag{4.46}$$

and since (u^n, v^n) satisfies the third equality in (4.45) together with (4.32), (u,v) satisfies $\sup\limits_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} (u+v) = \nu$. In particular, (u,v) is nontrivial and thus positive by the strong maximum principle.

Now, applying Lemma 4.5.3 to (u,v) with the positive constant $\alpha := \frac{1}{2}\min\left(\inf\limits_{x\in(-a_0,a_0)} (u(0,x), v(0,x)), \alpha_0\right)$, we get

$$\forall t > 0, \forall x \in (-a_0, a_0), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha \Phi^{a_0}(x).$$

Next, thanks to standard elliptic estimates, the sequence

$$(u^n(t,x), v^n(t,x)) := (u(t+n,x), v(t+n,x))$$

converges, up to an extraction, to a solution (u,v) of (4.46) — that we denote again by (u,v)— which satisfies

$$\sup_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} (u+v) \leq \nu, \tag{4.47}$$

and

$$\forall (t,x) \in \mathbb{R} \times (-a_0, a_0), \begin{pmatrix} u(t,x) \\ v(t,x) \end{pmatrix} \geq \alpha \Phi^{a_0}(x).$$

In particular, since $a_0 > a_1$, the latter implies

$$\inf_{(t,x)\in\mathbb{R}\times(-a_1,a_1)} \min(u,v) > 0. \tag{4.48}$$

Case 2: $\kappa_n \to \kappa \in (0, +\infty)$. Thanks to standard elliptic estimates, the sequence (u^n, v^n) converges, up to an extraction, to a solution (u, v) of

$$\begin{cases} -\kappa u_{tt} - u_{xx} + u_t &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \\ -\kappa v_{tt} - v_{xx} + v_t &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v, \end{cases} \tag{4.49}$$

and since (u^n, v^n) satisfies the third equality in (4.31) together with (4.32), (u, v) satisfies $\sup_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} (u+v) = \nu$. In particular, (u, v) is nontrivial and thus positive by the strong maximum principle.

Now, using Lemma 4.5.3 and a positive large shift in time exactly as in Case 1, we end up with a solution (u, v) to (4.49) which satisfies (4.47) and (4.48).

Case 3: $\kappa_n \to 0$. In this case, the elliptic operator becomes degenerate as $n \to \infty$, so that we cannot use the standard elliptic theory. The idea is then to use a Bernstein interior gradient estimate for elliptic systems that we present and prove in Appendix 4.6.2.

Applying Lemma 4.6.4 to the series (u^n, v^n) solving (4.31), we get a uniform L^∞ bound for (u_x^n, v_x^n). Furthermore by differentiating (4.31) with respect to x, we see that (u_x^n, v_x^n) solves a system for which Lemma 4.6.4 still applies. As a result, we get a uniform L^∞ bound for (u_{xx}^n, v_{xx}^n).

Let us show that there is also a uniform L^∞ bound for (u_t^n, v_t^n). From the uniform bounds found above, we can write

$$u_t^n - \kappa_n u_{tt}^n = F^n(t, x).$$

Let $F := \max(1, \sup_n \|F^n\|_{L^\infty(\mathbb{R}^2)}) < +\infty$. Assume by contradiction that there is a point (t_0, x_0) where $u_t^n(t_0, x_0) > 2F$. From the above equation we deduce that $u_t^n(t, x_0) > 2F$ remains valid for $t \geq t_0$, and thus

$$\kappa_n u_{tt}^n(t, x_0) > F, \quad \forall t \geq t_0.$$

Integrating twice, we get

$$u^n(t, x_0) \geq F(2(t - t_0) + \frac{1}{2\kappa_n}(t - t_0)^2) - \|u^n\|_{L^\infty}, \quad \forall t \geq t_0.$$

Letting $t \to \infty$ we get that u^n is unbounded, a contradiction. Thus, $u_t^n(t, x) \leq 2F$ for any $(t, x) \in \mathbb{R}^2$ and, in a straightforward way, this shows $|u_t^n(t, x)|, |v_t^n(t, x)| \leq 2F$ for any $(t, x) \in \mathbb{R}^2$.

Since we have uniform L^∞ bounds for (u^n, v^n), (u_x^n, v_x^n) and (u_t^n, v_t^n), there are u and v in $H^1_{loc}(\mathbb{R}^2)$ such that, up to a subsequence,

$$(u^n, v^n) \to (u, v) \text{ in } L^\infty_{loc}(\mathbb{R}^2), \quad (u_x^n, v_x^n, u_t^n, v_t^n) \rightharpoonup (u_x, v_x, u_t, v_t) \text{ in } L^2_{loc}(\mathbb{R}^2) \text{ weak.}$$

As a result, letting $n \to \infty$ into (4.31) yields

$$\begin{cases} u_t - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \\ v_t - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v \end{cases} \tag{4.50}$$

in a weak sense. From parabolic regularity, (u, v) is actually a classical solution to (4.50). Since the convergence occurs locally uniformly (4.32) and since (u^n, v^n) satisfies the third equality in (4.31) together with (4.32), (u, v) satisfies $\sup_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} (u+v) = \nu$. In particular, (u, v) is nontrivial and thus positive by the strong maximum principle.

Now, using Lemma 4.5.3 and a positive large shift in time as in Case 1 (parabolic estimates replacing elliptic estimates), we end up with a solution (u, v) to (4.50) which satisfies (4.47) and (4.48).

Conclusion. In any of the three above cases, we have constructed a classical solution (u, v) to ($\beta \geq 0$, $\kappa \geq 0$)

$$\begin{cases} \beta u_t - \kappa u_{tt} - u_{xx} &= u(r_u - \gamma_u(u+v)) + \mu v - \mu u \\ \beta v_t - \kappa v_{tt} - v_{xx} &= v(r_v - \gamma_v(u+v)) + \mu u - \mu v, \end{cases}$$

which satisfies (4.47) and (4.48). Applying Lemma 4.5.2, we find that (recall that $a_1 > a_0^*$)

$$\inf_{\mathbb{R}\times(-a_0^*,a_0^*)} (u, v) \geq \alpha_0 \inf_{(-a_0^*,a_0^*)} (\varphi^{a_1}, \psi^{a_1}) = \underline{\nu}.$$

But, since $a_0 > a_0^*$ the above implies

$$\sup_{\mathbb{R}\times(-a_0,a_0)} (u+v) \geq 2 \inf_{\mathbb{R}\times(-a_0^*,a_0^*)} (u, v) \geq 2\underline{\nu} > \nu^* > \nu,$$

which contradicts (4.47). Lemma 4.5.4 is proved. □

We are now in the position to prove Theorem 4.5.1.

Proof of Theorem 4.5.1. From the beginning of Section 4.5 and Lemma 4.5.4 we can consider a sequence $(\varepsilon_n, c_n, u^n(t,x), v^n(t,x))$ such that $\varepsilon_n > 0$, $\varepsilon_n \to 0$, $0 < c_n \leq \bar{c}^{\varepsilon_n} + \varepsilon_n$, (u^n, v^n) is a positive solution to problem (4.31) with $\varepsilon = \varepsilon_n$, $c = c_n$, $\nu < \nu^*$ and $a_0 > a_1$, satisfying the constraint (4.6), and the crucial fact

$$\lim_{n\to\infty} c_n > 0. \tag{4.51}$$

Notice that, as a by-product, this shows that $\bar{c}^0 := \lim_{\varepsilon\to 0} \bar{c}^\varepsilon > 0$ (see Lemma 4.4.2). We can now repeat the argument in the proof of Lemma 4.5.4 Case 3 and extract a sequence (u^n, v^n) which converges to a classical solution (u, v) of equation (4.33), satisfying the normalization

$$\sup_{x-ct\in(-a_0,a_0)} (u+v) = \nu$$

as well as the constraint (4.6). Theorem 4.5.1 is proved. □

4.5.3 Proof of Theorem 4.2.6

We are now close to conclude the proof of our main result of construction of a pulsating front, Theorem 4.2.6. From Theorem 4.5.1, it only remains to prove the boundary conditions (4.7), namely

$$\liminf_{t\to+\infty}\begin{pmatrix}u(t,x)\\ v(t,x)\end{pmatrix} > \begin{pmatrix}0\\0\end{pmatrix}, \quad \lim_{t\to-\infty}\begin{pmatrix}u(t,x)\\ v(t,x)\end{pmatrix} = \begin{pmatrix}0\\0\end{pmatrix},$$

locally uniformly with respect to x, to match Definition 4.2.5 of a pulsating front. The former is derived by another straighforward application of Lemma 4.5.3, while the latter is proved below. Hence, Theorem 4.2.6 is proved. $\square$

Lemma 4.5.5 (Zero limit behavior)**.** *For $a_1 > a_0^*$ and $\nu^* > 0$ as in subsection 4.5.2, let $c > 0$ and (u,v) be as in Theorem 4.5.1, satisfying in particular the normalization $\sup_{x-ct\in(-a_0,a_0)} (u+v) = \nu$ with $\nu < \nu^*$ and $a_0 > a_1$. Then*

$$\lim_{t\to-\infty} \max(u,v)(t,x) \to 0, \quad \textit{locally uniformly w.r.t. } x.$$

Proof. We first claim that $\inf_{\mathbb{R}\times(-a_0,a_0)} \min(u,v) = 0$. Indeed if this is not the case then, in particular, $\inf_{\mathbb{R}\times(-a_1,a_1)} \min(u,v) > 0$, and we derive a contradiction via Lemma 4.5.2 by a straightforward adaptation of the Conclusion of the proof of Lemma 4.5.4, because $\mathbb{R}\times(-a_1,a_1)$ intersects $\{(t,x) : x - ct \in (-a_0,a_0)\}$.

Now let $a > a_0$ be given and assume by contradiction that there is $m > 0$ and a sequence $t_n \to -\infty$ such that $\sup_{x\in(-a,a)} \max(u,v)(t_n,x) \geq m$. Thanks to the Harnack inequality for parabolic systems, see [90, Theorem 3.9], there is $C > 0$ such that

$$\forall n\in\mathbb{N}, \quad \inf_{x\in(-a,a)} \min(u,v)(t_n+1,x) \geq \frac{1}{C}\sup_{x\in(-a,a)} \max(u+v)(t_n,x) \geq \frac{m}{C}.$$

We now use our forward-in-time lower estimate, see Lemma 4.5.3, in $(-a,a)$ and with $\alpha := \frac{1}{2}\min(\alpha_0, \frac{m}{C}) > 0$ to get

$$\forall n\in\mathbb{N},\ \forall t > t_n+1,\ \forall x\in(-a,a),\ \begin{pmatrix}u(t,x)\\ v(t,x)\end{pmatrix} \geq \alpha\begin{pmatrix}\varphi^a(x)\\ \psi^a(x)\end{pmatrix}.$$

Since $t_n \to -\infty$ and $a > a_0$, the above implies

$$\inf_{(t,x)\in\mathbb{R}\times(-a_0,a_0)} \min(u,v)(t,x) \geq \alpha \inf_{x\in(-a_0,a_0)} (\varphi^a,\psi^a)(x) > 0.$$

This is a contradiction and the lemma is proved. $\square$

4.6 Appendix

4.6.1 Topological theorems

Let us first recall the classical Krein-Rutman theorem.

Theorem 4.6.1 (Krein-Rutman theorem). *Let E be a Banach space. Let $C \subset E$ be a closed convex cone of vertex 0, such that $C \cap -C = \{0\}$ and $Int\, C \neq \varnothing$. Let $T : E \to E$ be a linear compact operator such that $T(C\backslash\{0\}) \subset Int\, C$.*

Then, there exists $u \in Int\, C$ and $\lambda_1 > 0$ such that $Tu = \lambda_1 u$. Moreover, if $Tv = \mu v$ for some $v \in C\backslash\{0\}$, then $\mu = \lambda_1$. Finally, we have

$$\lambda_1 = \max\{|\mu|, \mu \in \sigma(T)\},$$

and the algebraic and geometric multiplicity of λ_1 are both equal to 1.

We now quote some results on the structure of the solution set for nonlinear eigenvalue problems in a Banach space, more specifically when bifurcation occurs. For more details and proofs, we refer the reader to the works of Rabinowitz [173, 174], Crandall and Rabinowitz [65]. See also earlier related results of Krasnosel'skii [144] and the book of Brown [50].

Theorem 4.6.2 (Bifurcation from eigenvalues of odd multiplicity). *Let E be a Banach space. Let $F : \mathbb{R} \times E \to E$ be a (possibly nonlinear) compact operator such that*

$$\forall \lambda \in \mathbb{R},\ F(\lambda, 0) = 0.$$

Assume that F is Fréchet differentiable near $(\lambda, 0)$ with derivative λT. Let us define

$$\mathcal{S} := \overline{\{(\lambda, x) \in \mathbb{R} \times E\backslash\{0\} : F(\lambda, x) = x\}}.$$

Let us assume that $\frac{1}{\mu} \in \sigma(T)$ is of odd multiplicity.

Then there exists a maximal connected component $\mathcal{C}_\mu \subset \mathcal{S}$ such that $(\mu, 0) \in \mathcal{C}_\mu$ and either

1. *$\mathcal{C}_\mu$ is not bounded in $\mathbb{R} \times E$, or*
2. *there exists $\mu^* \neq \mu$ with $\frac{1}{\mu^*} \in \sigma(T)$ and $(\mu^*, 0) \in \mathcal{C}_\mu$.*

When the eigenvalue is simple, one can actually refine the above result as follows.

Theorem 4.6.3 (Bifurcation from simple eigenvalues). *Let the assumptions of Theorem 4.6.2 hold. Assume further that $\frac{1}{\mu} \in \sigma(T)$ is simple. Let T^* be the dual of T, and $l \in E'$ an eigenvector of T^* associated with $\frac{1}{\mu}$ with $\|l\| = 1$ (recall that $\frac{1}{\mu}$ is of multiplicity 1 for both T and T^*). Let us define*

$$K^+_{\xi,\eta} := \{(\lambda, u) \in \mathbb{R} \times E, |\lambda - \mu| < \xi, \langle l, u \rangle > \eta \|u\|\}, \quad K^-_{\xi,\eta} := -K^+_{\xi,\eta}.$$

Then $\mathcal{C}_\mu \backslash \{(\mu,0)\}$ contains two connected components $\mathcal{C}_\mu^+$ and $\mathcal{C}_\mu^-$ which satisfy

$$\forall \nu \in \{+,-\}, \forall \xi > 0, \forall \eta \in (0,1), \exists \zeta_0 > 0, \forall \zeta \in (0,\zeta_0),\ (\mathcal{C}_\mu^\nu \cap B_\zeta) \subset K_{\xi,\eta}^\nu,$$

where $B_\zeta := \{(\lambda,u) \in \mathbb{R}\times E, |\lambda-\mu| < \zeta, \|u\| < \zeta\}$ is the ball of center $(\mu,0)$ and radius ζ. Moreover, $\mathcal{C}_\mu^+$ and $\mathcal{C}_\mu^-$ satisfy either item 1 or 2 in Theorem 4.6.2.

4.6.2 A Bernstein-type interior gradient estimate for elliptic systems

We present here some L^∞ gradient estimates for regularizations of degenerate elliptic systems, which are uniform with respect to the regularization parameter $\kappa \geq 0$. The result below generalizes the result of Berestycki and Hamel [19], which is concerned with scalar equations.

Lemma 4.6.4 (Interior gradient estimates)**.** *Let Ω be an open subset of $\mathbb{R}^2$. Let $f, g : \Omega \times \mathbb{R}^2 \to \mathbb{R}$ be two C^1 functions with bounded derivatives. Let $0 \leq \kappa \leq 1$ and $(u(y,x), v(y,x))$ be a solution of the class C^3 of the system*

$$\left\{ \begin{array}{rcll} -\kappa u_{yy} - u_{xx} + u_y &=& f(y,x,u,v) & \textit{in } \Omega, \\ -\kappa v_{yy} - v_{xx} + v_y &=& g(y,x,u,v) & \textit{in } \Omega. \end{array} \right. \tag{4.52}$$

Then, for all $(y,x) \in \Omega$,

$$|u_x(y,x)|^2 + |v_x(y,x)|^2 + \kappa|u_y(y,x)|^2 + \kappa|v_y(y,x)|^2 \leq C\left(1 + \frac{1}{(dist((y,x),\partial\Omega))^2}\right)$$

where

$$C = C(\|u\|_{L^\infty(B)} + \|v\|_{L^\infty(B)}, osc_B u, osc_B v, \|f\|_{C^{0,1}(B\times[\underline{u},\overline{u}]\times[\underline{v},\overline{v}])}, \|g\|_{C^{0,1}(B\times[\underline{u},\overline{u}]\times[\underline{v},\overline{v}])}),$$

with B the ball of center (y,x) and radius $\frac{dist((y,x),\partial\Omega)}{2}$ in $\mathbb{R}^2$, $\underline{u} := \inf_B u$, $\overline{u} := \sup_B u$, $\underline{v} := \inf_B v$, $\overline{v} := \sup_B v$. In particular, this estimate is independent on the regularization parameter $0 \leq \kappa \leq 1$.

Proof. Let h be the smooth function defined on $\mathbb{R}$ by

$$h(z) := \left\{ \begin{array}{ll} \exp\left(\frac{z^2}{z^2-1}\right) & |z| < 1 \\ 0 & |z| \geq 1. \end{array} \right.$$

Let us then define $C_0 := \max(\|h\|_{L^\infty}, \|h'\|_{L^\infty}, \|h''\|_{L^\infty})$ and $\zeta(Y,X) := h\left(\frac{\sqrt{Y^2+X^2}}{2}\right)$.

Let $(y_0, x_0) \in \Omega$ be a given point, $d_0 := dist((y_0, x_0), \partial\Omega)$ be the distance to $\partial\Omega$, $d := \min\left(\frac{d_0}{2}, 1\right)$, B_0 the ball of center (y_0, x_0) and radius d. Let χ be the function defined by

$$\forall (y,x) \in \mathbb{R}^2, \quad \chi(y,x) := \zeta\left(\frac{y-y_0}{d}, \frac{x-x_0}{d}\right).$$

Finally, let P^u and P^v be defined in Ω by

$$\begin{array}{rcl} P^u(y,x) & := & \chi^2(y,x)(u_x^2(y,x) + \kappa u_y^2(y,x)) + \lambda u^2(y,x) + \rho e^{x-x_0} \\ P^v(y,x) & := & \chi^2(y,x)(v_x^2(y,x) + \kappa v_y^2(y,x)) + \lambda v^2(y,x) + \rho e^{x-x_0}, \end{array}$$

where $\lambda > 0$ and $\rho > 0$ are constants to be fixed later. Our goal is to apply the maximum principle to the function $P := P^u + P^v$ for convenient values of λ and ρ. We present below the computations on P^u only and reflect them on P^v.

We first compute the partial derivatives of P^u and get

$$\begin{array}{rcl} P_y^u & = & 2\chi_y\chi u_x^2 + 2\chi^2 u_{xy}u_x + 2\kappa(\chi_y\chi u_y^2 + \chi^2 u_{yy}u_y) + 2\lambda u_y u \\ P_{yy}^u & = & 2(\chi_{yy}\chi + \chi_y^2)u_x^2 + 8\chi_y\chi u_{xy}u_x + 2\chi^2(u_{xyy}u_x + u_{xy}^2) \\ & & +\kappa[2(\chi_{yy}\chi + \chi_y^2)u_y^2 + 8\chi_y\chi u_{yy}u_y + 2\chi^2(u_{yyy}u_y + u_{yy}^2)] \\ & & +2\lambda(u_{yy}u + u_y^2) \\ P_{xx}^u & = & 2(\chi_{xx}\chi + \chi_x^2)u_x^2 + 8\chi_x\chi u_{xx}u_x + 2\chi^2(u_{xxx}u_x + u_{xx}^2) \\ & & \kappa[2(\chi_{xx}\chi + \chi_x^2)u_y^2 + 8\chi_x\chi u_{xy}u_y + 2\chi^2(u_{yxx}u_y + u_{yx}^2)] \\ & & +2\lambda(u_{xx}u + u_x^2) + \rho e^{x-x_0}. \end{array}$$

Let $M := \partial_y - \kappa\partial_{yy} - \partial_{xx}$. Then we have

$$\begin{array}{rcl} MP^u & = & 2\left[\chi_y\chi - \kappa(\chi_{yy}\chi + \chi_y^2) - (\chi_{xx}\chi + \chi_x^2)\right]u_x^2 \\ & & +2\kappa\left[\chi_y\chi - \kappa(\chi_{yy}\chi + \chi_y^2) - (\chi_{xx}\chi + \chi_x^2)\right]u_y^2 \\ & & +2\chi^2\left[u_{xy} - \kappa u_{xyy} - u_{xxx}\right]u_x \\ & & +2\kappa\chi^2\left[u_{yy} - \kappa u_{yyy} - u_{yxx}\right]u_y \\ & & -2\left[\kappa(\chi^2 u_{xy}^2 + 4\chi_y\chi u_{xy}u_x) + (\chi^2 u_{xx}^2 + 4\chi_x\chi u_{xx}u_x)\right] \\ & & -2\kappa[\kappa(4\chi_y\chi u_y u_{yy} + \chi^2 u_{yy}^2) + (4\chi_x\chi u_y u_{xy} + \chi^2 u_{xy}^2)] \\ & & +2\lambda\left[(u_y - \kappa u_{yy} - u_{xx})u - \kappa u_y^2 - u_x^2\right] \\ & & -\rho e^{x-x_0}. \end{array}$$

We now reformulate some of the lines of the above equality, starting with lines three and four. We differentiate the first equation of system (4.52) with respect to x to obtain

$$\begin{aligned} 2\chi^2\left[u_{xy} - \kappa u_{xyy} - u_{xxx}\right]u_x &= 2\chi^2(f_x + u_x f_u + v_x f_v)u_x \\ &\le \chi^2(u_x^2 + f_x^2) + 2\chi^2 u_x^2|f_u| + \chi^2(u_x^2 + v_x^2)|f_v|, \end{aligned}$$

and then with respect to y to get

$$\begin{aligned}2\chi^2\left[u_{yy}-\kappa u_{yyy}-u_{yxx}\right]u_y &= 2\chi^2(f_y+u_yf_u+v_yf_v)u_y\\ &\le \chi^2(u_y^2+f_y^2)+2\chi^2u_y^2|f_u|+\chi^2(u_y^2+v_y^2)|f_v|.\end{aligned}$$

As far as lines five and six are concerned, we use the factorizations

$$\begin{aligned}\chi^2u_{xy}^2+4\chi_y\chi u_{xy}u_x &= (\chi u_{xy}+2\chi_yu_x)^2-4\chi_y^2u_x^2\\ \chi^2u_{xx}^2+4\chi_x\chi u_{xx}u_x &= (\chi u_{xx}+2\chi_xu_x)^2-4\chi_x^2u_x^2\\ \chi^2u_{yy}^2+4\chi_y\chi u_{yy}u_y &= (\chi u_{yy}+2\chi_yu_y)^2-4\chi_y^2u_y^2\\ \chi^2u_{xy}^2+4\chi_x\chi u_{xy}u_y &= (\chi u_{xy}+2\chi_xu_y)^2-4\chi_x^2u_y^2.\end{aligned}$$

For line seven, we use the first equation in (4.52) to write $(u_y-\kappa u_{yy}-u_{xx})u = fu$. As a result, we collect

$$\begin{aligned}MP^u \le{}& 2\left[\chi_y\chi-\kappa\chi_{yy}\chi-\chi_{xx}\chi+3\chi_x^2+3\kappa\chi_y^2+\chi^2\left(|f_u|+\frac{1+|f_v|}{2}\right)-\lambda\right]\\ &\times(u_x^2+\kappa u_y^2)+2\lambda fu+\chi^2(v_x^2+\kappa v_y^2)|f_v|+\chi^2(f_x^2+\kappa f_y^2)-\rho e^{x-x_0},\end{aligned}$$

and, similarly,

$$\begin{aligned}MP^v \le{}& 2\left[\chi_y\chi-\kappa\chi_{yy}\chi-\chi_{xx}\chi+3\chi_x^2+3\kappa\chi_y^2+\chi^2\left(|g_v|+\frac{1+|g_u|}{2}\right)-\lambda\right]\\ &\times(v_x^2+\kappa v_y^2)+2\lambda gv+\chi^2(u_x^2+\kappa u_y^2)|g_u|+\chi^2(g_x^2+\kappa g_y^2)-\rho e^{x-x_0}.\end{aligned}$$

Notice that $|\chi|\le C_0$, $|\chi_x|,|\chi_y|\le\frac{C_0}{d}$, $|\chi_{xx}|,|\chi_{yy}|\le\frac{C_0}{d^2}$ and recall that $\kappa,d\le 1$. Hence, putting everything together, we arrive at

$$\begin{aligned}MP \le{}& \left(20\frac{C_0^2}{d^2}+4C_0^2(\|f\|_{C^{0,1}}+\|g\|_{C^{0,1}})+C_0^2-\lambda\right)(u_x^2+v_x^2+\kappa u_y^2+\kappa v_y^2)\\ &+2\lambda(\|f\|_{L^\infty}+\|g\|_{L^\infty})(\|u\|_{L^\infty}+\|v\|_{L^\infty})+2C_0^2(\|f\|_{C^{0,1}}^2+\|g\|_{C^{0,1}}^2)-2\rho e^{x-x_0}.\end{aligned}$$

It is now time to specify

$$\begin{cases}\lambda = 20\frac{C_0^2}{d^2}+4C_0^2(\|f\|_{C^{0,1}}+\|g\|_{C^{0,1}})+C_0^2>0\\ \rho = \frac{e}{2}\big[2\lambda(\|f\|_{L^\infty}+\|g\|_{L^\infty})(\|u\|_{L^\infty}+\|v\|_{L^\infty})\\ \qquad\qquad +2C_0^2(\|f\|_{C^{0,1}}^2+\|g\|_{C^{0,1}}^2)+1\big]>0.\end{cases}$$

As a result we have $MP(y,x)<0$ for all $(y,x)\in B_0$ (since then $x-x_0\ge -1$). The maximum principle then implies

$$P(y_0,x_0)\le\max_{(y,x)\in\partial B_0}P(y,x).$$

Since $\chi(y_0,x_0)=1$ and $\chi(y,x)=0$ when $(y,x)\in\partial B_0$, the above inequality implies

$$\begin{aligned}(u_x^2+v_x^2+\kappa u_y^2+\kappa v_y^2)(y_0,x_0) &\le \lambda(\|u\|_{L^\infty}^2+\|v\|_{L^\infty}^2)-\lambda(u^2+v^2)(y_0,x_0)+2\rho e\\ &\le 2\lambda(\|u\|_{L^\infty} osc_{B_0}(u)+\|v\|_{L^\infty} osc_{B_0}(v))+2\rho e\\ &\le K\Big((\|u\|_{L^\infty}+\|v\|_{L^\infty})\big(osc_{B_0}(u)+osc_{B_0}(v)\\ &\quad+\|f\|_{C^{0,1}}+\|g\|_{C^{0,1}}\big)+\|f\|_{C^{0,1}}^2+\|g\|_{C^{0,1}}^2+1\Big)\left(1+\frac{1}{d^2}\right)\end{aligned}$$

using the expressions of λ and ρ above, for a universal positive constant $K>0$ and where the $C^{0,1}$ norms of f, g are taken on $B_0\times[\inf_{B_0}u,\sup_{B_0}u]\times[\inf_{B_0}v,\sup_{B_0}v]$. This proves the lemma. □

4.6.3 Dirichlet and periodic principal eigenvalues

We prove here that the principal eigenvalue with Dirichlet boundary conditions in a ball converges to the principal eigenvalue with periodic boundary conditions, when the radius tends to $+\infty$.

Lemma 4.6.5 (Dirichlet and periodic principal eigenvalues)**.** *Let the matrix field $A\in L^\infty(\mathbb{R};\mathcal{S}_2(\mathbb{R}))$ be symmetric, cooperative and periodic with period $L>0$. Let λ_1 be the principal eigenvalue of the operator $-\partial_{xx}-A(x)$ with periodic boundary conditions, that is*

$$-\begin{pmatrix}\varphi\\ \psi\end{pmatrix}''-A(x)\begin{pmatrix}\varphi\\ \psi\end{pmatrix}=\lambda_1\begin{pmatrix}\varphi\\ \psi\end{pmatrix}, \tag{4.53}$$

with $\varphi,\psi\in H^1_{per}$ and $\varphi>0,\psi>0$. For $R>0$, let λ_1^R be the principal eigenvalue of the operator $-\partial_{xx}-A(x)$ with Dirichlet boundary conditions on $(-R,R)$, that is

$$-\begin{pmatrix}\varphi^R\\ \psi^R\end{pmatrix}''-A(x)\begin{pmatrix}\varphi^R\\ \psi^R\end{pmatrix}=\lambda_1^R\begin{pmatrix}\varphi^R\\ \psi^R\end{pmatrix}, \tag{4.54}$$

with $\varphi^R,\psi^R\in H^1_0(-R,R)$ and $\varphi^R>0,\psi^R>0$. Then, there exists $C>0$ depending only on A such that, for all $R>0$,

$$\lambda_1\le\lambda_1^R\le\lambda_1+\frac{C}{R}.$$

Proof. Without loss of generality we assume $L=1$. Inequality $\lambda_1\le\lambda_1^R$ is very classical, see [21, Proposition 4.2] or [2, Proposition 3.3] for instance, and we omit the details. Also, the same classical argument yields that $R\mapsto\lambda_1^R$ is nonincreasing so it is enough to prove $\lambda_1^R\le\lambda_1+\frac{C}{R}$ when $R=2,3,\ldots$.

We consider a smooth auxiliary function $\eta : \mathbb{R} \to \mathbb{R}$ satisfying

$$\eta \equiv 1 \text{ on } (-\infty, 0],\ 0 < \eta < 1 \text{ on } (0,1),\ \eta \equiv 0 \text{ on } [1, \infty).$$

Since the operator in (4.54) is self-adjoint in the domain $(-R, R)$, the principal eigenvalue λ_1^R is given by the Rayleigh quotient

$$\lambda_1^R = \inf_{\Psi \in \mathbf{H}_0^1(-R,R), \Psi \neq 0} Q(\Psi, \Psi), \quad Q(\Psi, \Psi) := \frac{\int_{-R}^{R} ({}^t\Psi_x \Psi_x - {}^t\Psi A(x) \Psi) \mathrm{d}x}{\int_{-R}^{R} {}^t\Psi \Psi \mathrm{d}x}.$$

In particular we have $\lambda_1^R \leq Q(\Theta, \Theta)$, with Θ the $\mathbf{H}_0^1(-R, R)$ test function defined by

$$\Theta(x) := \eta(-R+1-x)\eta(-R+1+x)\Phi(x), \quad \Phi(x) := \begin{pmatrix} \varphi(x) \\ \psi(x) \end{pmatrix},$$

where φ, ψ are as in (4.53), with the normalization $\int_0^1 {}^t\Phi\Phi \mathrm{d}x = 1$. We then have $Q(\Theta, \Theta) = Q^1(\Theta) + Q^2(\Theta)$, where

$$Q^1(\Theta) := \frac{\int_{|x| \leq R-1} ({}^t\Theta_x \Theta_x - {}^t\Theta A(x) \Theta) \mathrm{d}x}{\int_{-R}^{R} {}^t\Theta\Theta \mathrm{d}x},$$

$$Q^2(\Theta) := \frac{\int_{R-1 \leq |x| \leq R} ({}^t\Theta_x \Theta_x - {}^t\Theta A(x) \Theta) \mathrm{d}x}{\int_{-R}^{R} {}^t\Theta\Theta \mathrm{d}x}.$$

We write

$$\begin{aligned} Q^1(\Theta) &= \frac{\int_{|x| \leq R-1} ({}^t\Theta_x \Theta_x - {}^t\Theta A(x) \Theta) \mathrm{d}x}{\int_{|x| \leq R-1} {}^t\Theta\Theta \mathrm{d}x} \frac{\int_{-(R-1)}^{R-1} {}^t\Theta\Theta \mathrm{d}x}{\int_{-R}^{R} {}^t\Theta\Theta \mathrm{d}x} \\ &= \lambda_1 \frac{\int_{-(R-1)}^{R-1} {}^t\Theta\Theta \mathrm{d}x}{\int_{-R}^{R} {}^t\Theta\Theta \mathrm{d}x}, \end{aligned}$$

thanks to $\Theta \equiv \Phi \equiv \begin{pmatrix} \varphi \\ \psi \end{pmatrix}$ on $(-(R-1), R-1)$ and the 1-periodicity of φ, ψ (recall that $R-1$ is an integer). As a result

$$|Q^1(\Theta) - \lambda_1| = |\lambda_1| \frac{\int_{R-1<|x|<R} {}^t\Theta\Theta \mathrm{d}x}{\int_{-R}^{R} {}^t\Theta\Theta \mathrm{d}x} \leq |\lambda_1| \frac{\int_{R-1<|x|<R} {}^t\Phi\Phi \mathrm{d}x}{\int_{-(R-1)}^{R-1} {}^t\Phi\Phi \mathrm{d}x} = |\lambda_1| \frac{1}{R-1},$$

since $0 \leq \eta \leq 1$. On the other hand one can see that, for a constant $C_2 > 0$ depending only on $\|\eta'\|_{L^\infty(\mathbb{R})}$ and $\|A\|_{L^\infty(\mathbb{R}; \mathcal{S}_2(\mathbb{R}))}$,

$$\begin{aligned} \left| \int_{R-1<|x|<R} ({}^t\Theta_x \Theta_x - {}^t\Theta A(x) \Theta) \mathrm{d}x \right| &\leq C_2 \int_{R-1<|x|<R} ({}^t\Phi\Phi + {}^t \Phi_x \Phi_x) \mathrm{d}x \\ &= 2C_2 \int_{0<|x|<1} ({}^t\Phi\Phi + {}^t \Phi_x \Phi_x) \mathrm{d}x =: C_2' \end{aligned}$$

so that

$$|Q^2(\Theta)| \leq \frac{C_2'}{\int_{-R}^{R} {}^t\Theta\Theta \mathrm{d}x} \leq \frac{C_2'}{\int_{-(R-1)}^{R-1} {}^t\Phi\Phi \mathrm{d}x} = \frac{C_2'}{(2R-2)\int_0^1 {}^t\Phi\Phi \mathrm{d}x} = \frac{C_2'}{(2R-2)}.$$

This concludes the proof of the lemma. □

Chapitre 5

Singular measure traveling waves in a nonlocal reaction-diffusion equation

5.1 Introduction

In this work we are interested in the problem:

$$u_t = u_{xx} + \mu(M \star u - u) + u(a(y) - K \star u) \tag{5.1}$$

where $u = u(t, x, y)$ represents the density of a population with $t > 0$ being the time, $x \in \mathbb{R}$ the space and $y \in \Omega$ a phenotypic trait. The function $a(y)$ represents the fitness of trait y in the absence of competition; the function $K = K(y, z)$ represents the strength of the competition occuring between trait y and trait z, while the function $M = M(y, z)$ represents mutations occuring inside the population, modifying trait y to trait z at rate μ. Notice that $\star$ is not the standard convolution (see below for details). In the context of epidemiology, where $u(t, x, y)$ can be thought as a density of hosts infected with a pathogen of trait y, $M(y, z)$ represents the probability that a pathogen of trait z appears inside a host infected with y and takes over the infection.

We are particularly interested in constructing traveling waves for equation (5.1) for which $u(x-ct, \cdot)$ is a Radon measure on $\overline{\Omega}$ for almost every t, x. We do not expect more regularity to hold in trait for a general fitness function a, since it is known that in some cases, the principal eigenvalue (which drives the behaviour of the front) associated with (5.1) is singular. In the introduction we give an explicit construction of a singular traveling wave when the competition kernel $K(y, z)$ is independent from the y variable.

5.2 Main results and comments

5.2.1 Function spaces and basic notions

Throughout this document we use a number of function spaces that we precise here to avoid any confusion. Whenever X is a subset of a Euclidian space, we will denote $C(X)$, $C_b(X)$, $C_0(X)$, $C_c(X)$ the space of continuous functions, bounded continuous functions, continuous functions vanishing at ∞ and continuous functions with compact support over X, respectively. Notice that if X is compact, then those four function spaces coincide. Whenever $X \subset \mathbb{R}^d$ is a Borel set, we define $M^1(X)$ as the set of all Borel-regular measures over X. Let us recall that $M^1(X)$ is the topological dual of $C_0(X)$, thanks to Riesz's representation theorem [184]. In our context, $M^1(X)$ coincides with the set of Borel measures that are inner and outer regular [184, 36]. We will thus call *Radon measure* an element of $M^1(X)$.

When $p \in M^1(X)$, we say that the equality $p = 0$ holds *in the sense of measures* if

$$\forall \psi \in C_c(X), \int_X \psi(x)p(dx) = 0.$$

We now define the notion of *transition kernel* (see [36, Definition 10.7.1]), which is crucial for our notion of traveling wave:

Definition 5.2.1 (Transition kernel)**.** We say that $u \in M^1(\mathbb{R} \times X)$ has a *transition kernel* if there exists a function $k(x, dy)$ such that

1. for any Borel set $A \subset X$, $k(\cdot, A)$ is a measurable function, and
2. for almost every $x \in \mathbb{R}$ (with respect to the Lebesgue measure on $\mathbb{R}$), $k(x, \cdot) \in M^1(X)$

and $u(dx, dy) = k(x, dy)dx$ in the sense of measures, i.e. for any test function $\varphi \in C_c(\mathbb{R} \times X)$, the following equality holds

$$\int_{\mathbb{R}\times X} \varphi(x, y)u(dx, dy) = \int_{\mathbb{R}} \int_X \varphi(x, y)k(x, dy)dx.$$

For simplicity, if the measure u has a transition kernel, we will often say that u *is* a transition kernel and use directly the notation $u(dx, dy) = u(x, dy)dx$.

We will denote $f \star g$ the function:

$$f \star g(y) := \int_{\Omega} f(y, z)g(dz)$$

whenever $f : \overline{\Omega}^2 \to \mathbb{R}$ and g is a measure on $\overline{\Omega}$. If g is continuous or $L^1(\Omega)$ we use the convention $g(dz) := g(z)dz$ in the above formula. Remark that the operation $\star$ is not the standard convolution, though both notions share many properties.

5.2.2 Main results

Our main result is the existence of a measure traveling wave, possibly singular, for equation (5.1). Before a precise statement, let us give our assumptions, as well as subsidiary results.

Assumption 5.2.2 (Minimal assumptions).

1. $\Omega \subset \mathbb{R}^n$ is a bounded connected open set with C^3 boundary. For simplicity we assume $0 \in \Omega$.

2. $M = M(y,z)$ is a $C^{0,\alpha}$ positive function $\overline{\Omega} \times \overline{\Omega} \to \mathbb{R}$ satisfying

$$\forall z \in \overline{\Omega}, \int_{\overline{\Omega}} M(y,z)dy = 1.$$

   In particular, we have

$$\forall (y,z) \in \overline{\Omega} \times \overline{\Omega}, \quad 0 < m_0 \leq M(y,z) \leq m_\infty < +\infty.$$

3. $K = K(y,z)$ is a $C^{0,\alpha}$ positive function $\overline{\Omega} \times \overline{\Omega} \to \mathbb{R}$. In particular, we have

$$\forall (y,z) \in \overline{\Omega} \times \overline{\Omega}, \quad 0 < k_0 \leq K(y,z) \leq k_\infty < +\infty$$

4. $a = a(y)$ is a $C^{0,\alpha}$ function $\overline{\Omega} \to \mathbb{R}$ with $a(0) = \sup_{y \in \overline{\Omega}} a(y) > 0$. We assume that a is non-constant. In particular, we have $-\infty < \inf a < \sup a < +\infty$.

5. We let

$$\Omega_0 := \left\{ y \in \overline{\Omega}, a(y) = a(0) = \sup_{z \in \overline{\Omega}} a(z) \right\}$$

   and assume $\Omega_0 \subset\subset \Omega$.

6. $0 < \mu < \sup a$.

We are particularly interested in a more restrictive set of assumptions, under which we hope to see a concentration phenomenon in (5.1):

Assumption 5.2.3 (Concentration hypothesis). In addition to Assumption 5.2.2, we suppose

$$y \mapsto \frac{1}{\sup_{z \in \Omega} a(z) - a(y)} \in L^1(\Omega).$$

Let us introduce the principal eigenvalue problem that guides our analysis:

Definition 5.2.4 (Principal eigenvalue)**.** We call *principal eigenvalue* associated with (5.1) the real number:

$$\lambda_1 := \sup\{\lambda, \exists \varphi \in C(\overline{\Omega}), \varphi > 0 \text{ s.t. } \mu(M \star \varphi - \varphi) + (a(y) + \lambda)\varphi \leq 0\}. \tag{5.2}$$

Clearly, λ_1 is well-defined and $\lambda_1 \leq -(\sup a - \mu)$ by evaluating (5.2) at $y = 0$. Though we call λ_1 the principal eigenvalue, we stress that λ_1 is not always associated with a usual eigenfunction. In particular, Coville, in his work [61, 60], gives conditions on the coefficients of (5.1) under which there exists no associated eigenfunction. We will recall and precise these results in section 5.3.1. In particular, we recall that

Proposition 5.2.5 (On the principal eigenvalue)**.** *Under Assumption 5.2.2, there exists a unique* $\lambda \in \mathbb{R}$ *such that the equation*

$$\mu(M \star \varphi - \varphi) + (a(y) + \lambda)\varphi = 0 \tag{5.3}$$

has a nonnegative nontrivial solution in the sense of measures, and $\lambda = \lambda_1$*.*

Moreover, under Assumption 5.2.3, there exists $\mu_0 > 0$ *such that if* $\mu < \mu_0$*, we have*

$$\lambda_1 = -(\sup a - \mu)$$

and, in this case, there exists a nonnegative measure φ *solution to* (5.3) *with a singluar part concentrated in* Ω_0*.*

As well-known in KPP situations, we expect the sign of λ_1 to dictate the long-time persistence of solutions to equation (5.1). In particular, when $\lambda_1 > 0$, we expect that any nonnegative solution to the Cauchy problem (5.1) starting from a positive bounded initial condition goes to 0 as $t \to \infty$. Indeed, in this case there exists a positive continuous function $\psi > 0$ such that

$$\mu(M \star \psi - \psi) + \left(a + \frac{\lambda_1}{2}\right)\psi \leq 0.$$

The result is then a consequence of the comparison principle satisfied by the linear equation

$$u_t = u_{xx} + \mu(M \star u - u) + a(y)u.$$

Indeed, one can check that $Ce^{-\frac{\lambda_1}{4}t}\psi(y)$ and $u(t,x,y)$ are respectively a super- and subsolution of the above equation with ordered initial data (for C large enough).

In the present paper we focus on the $\lambda_1 < 0$ case, in which we expect survival of the population. To confirm this scenario, we first prove the existence of a nonnegative nontrivial stationary state for equation (5.1).

Theorem 5.2.6 (Survival of the population)**.** *Let Assumption 5.2.2 hold and assume* $\lambda_1 < 0$*. Then, there exists a nonnegative nontrivial stationary state for equation* (5.1)*, i.e. a nonnegative nontrivial measure* $p \in M^1(\overline{\Omega})$ *which satisfies*

$$\mu(M \star p - p) + p(a(y) - K \star p) = 0 \tag{5.4}$$

in the sense of measures.

Under the hypothesis for concentration (Assumption 5.2.3) and in the special case where the competition kernel $K(y,z)$ is independent of the trait y, Bonnefon, Coville and Legendre [39] showed that the solution to (5.4) has a singularity concentrated in Ω_0 when μ is small. A key argument was a separation of variables trick, allowed by the assumption $K(y,z) = K(z)$. Here we show that the concentration phenomenon occurs under a more general hypothesis on K, namely that the trait $y \in \Omega_0$ suffers less from the competition than any other trait. Since Ω_0 also maximizes the basic reproductive ratio $a(y)$, it seems natural to expect concentration in Ω_0 in this case.

Assumption 5.2.7 (Nonlinear concentration hypothesis). In addition to Assumption 5.2.3, we suppose that

$$\forall (y,z) \in \overline{\Omega} \times \overline{\Omega}, \quad K(0,z) \leq K(y,z).$$

Theorem 5.2.8 (Concentration on dominant trait)**.** *Let Assumption 5.2.7 hold, and assume $\lambda_1 < 0$. Then, there exists $\mu_0 > 0$ such that, for any $\mu < \mu_0$, the measure p, constructed in Theorem 5.2.6, has a singular part concentrated in Ω_0.*

To better characterize the spatial dynamics of solutions to (5.1), we are going to construct traveling waves for (5.1).

Definition 5.2.9 (Traveling wave)**.** A *traveling wave* for equation (5.1) is a couple (c, u) where $c \in \mathbb{R}$ and u is a transition kernel (see Definition 5.2.1) defined on $\mathbb{R} \times \overline{\Omega}$ which is locally finite. We require that (c, u) satisfies:

$$-cu_x - u_{xx} = \mu(M \star u - u) + u(a - K \star u) \tag{5.5}$$

in the sense of distributions, and that the measure u satisfies the limit conditions:

$$\liminf_{\bar{x} \to +\infty} \int_{\mathbb{R} \times \overline{\Omega}} \psi(x + \bar{x}, y) u(dx, dy) > 0, \tag{5.6}$$

$$\limsup_{\bar{x} \to -\infty} \int_{\mathbb{R} \times \overline{\Omega}} \psi(x + \bar{x}, y) u(dx, dy) = 0 \tag{5.7}$$

for any positive test function $\psi \in C_c(\mathbb{R} \times \overline{\Omega})$.

We are now in the position to state our main result, which concerns the existence of a traveling wave for (5.1).

Theorem 5.2.10 (Existence of a traveling wave)**.** *Under Assumption 5.2.2, there exists a traveling wave (c, u) for (5.1) with $c = c^* := 2\sqrt{-\lambda_1}$.*

In the general case, it seems very involved to determine whether u has a singular part or not. Nevertheless, there are some particular cases where singular traveling waves do exist.

Remark 5.2.11 (Traveling waves with a singular part). In the special case where K is independent from y ($K(y,z) = K(z)$), a separation of variables argument — see [22] for a related trick— allows us to construct traveling waves that actually have a singular part in $\overline{\Omega}$. From Proposition 5.2.5, under Assumption 5.2.3, there is $\mu_0 >$ such that, for any $\mu < \mu_0$, there exists a measure eigenvector $\varphi \in M^1(\overline{\Omega})$ with a singular part concentrated in Ω_0. We choose such a φ with normalization $\int_{\overline{\Omega}} K(z)\varphi(dz) = 1$. If moreover $\lambda_1 < 0$, then there exists a positive front ρ, connecting $-\lambda_1$ to 0, for the Fisher-KPP equation

$$-\rho_{xx} - c\rho_x = \rho(-\lambda_1 - \rho) \tag{5.8}$$

for any $c \geq 2\sqrt{-\lambda_1}$. If we define $u(x,dy) := \rho(x)\varphi(dy)$, we see that u matches the definition of a traveling wave. Hence for any $x \in \mathbb{R}$, $u(x,\cdot)$ possesses a singular part concentrated in Ω_0.

The organization of the paper is as follows. In Section 5.3 we study related eigenvalue problems for which concentration may occur. Section 5.4 is devoted to the construction of stationary states through a bifurcation method. Last, we construct a (possibly singular) measure traveling wave in Section 5.5.

5.3 On some principal eigenvalue problems

In this section, we prove Proposition 5.2.5, which allows an approximation by an elliptic Neumann eigenvalue problem in Theorem 5.3.5 of crucial importance for the construction of steady states in Section 5.4.

5.3.1 The principal eigenvalue of nonlocal operators

Under Assumption 5.2.2, Coville *et al.* [60, 61, 62] have extensively studied the principal eigenvalue problem associated with (5.1), see Appendix 5.6.1. We summarize and precise the results in [61] under Assumption 5.2.3 of concentration. Our contribution is the uniqueness of the real number λ such that (5.3) has a weak solution in the sense of measures.

Theorem 5.3.1 (Principal eigenpairs and further properties)**.** *Let Assumption 5.2.3 hold. Then, λ_1 (defined by* (5.2)*) is the unique $\lambda \in \mathbb{R}$ such that equation* (5.3) *has a nontrivial weak solution (λ, φ) with $\varphi \in M^1(\overline{\Omega})$ and $\varphi \geq 0$.*

More precisely, let

$$\mathcal{M}[\psi] := \int_\Omega \mu M(y,z) \frac{\psi(z)}{\sup a - a(z)} dz$$

for $\psi \in C_b(\Omega)$, and let $\gamma_1 > 0$ be the first eigenvalue of the operator $\mathcal{M}$, so that there exists $\Phi \in C_b(\Omega)$ with $\Phi > 0$ and $\mathcal{M}[\Phi] = \gamma_1 \Phi$. Then the following holds:

(i) $\gamma_1 > 1$ *if, and only if,* $\lambda_1 < -(\sup a - \mu)$. *In this case, there exists a bounded continuous eigenfunction* $\varphi > 0$ *associated with* λ_1, *and any solution in the sense of measures to* (5.3) *is a continuous solution in the classical sense.*

(ii) $\gamma_1 = 1$ *if, and only if,* $\lambda_1 = -(\sup a - \mu)$ *and the function* $\varphi(y) = \frac{\Phi(y)}{\sup a - a(y)} \in L^1(\Omega)$ *is a solution to* (5.3) *almost everywhere. In this case,* φ *is the unique solution to* (5.3) *in the sense of measures (up to multiplication by a positive constant).*

(iii) $\gamma_1 < 1$ *if, and only if,* $\lambda_1 = -(\sup a - \mu)$ *and there exists a nonnegative measure* $\varphi \in M^1(\overline{\Omega})$ *solution to* (5.3) *which is singular with respect to the Lebesgue measure on* $\overline{\Omega}$. *In this case, any nonnegative nontrivial solution to* (5.3) *is singular with respect to the Lebesgue measure with a singularity concentrated in* Ω_0.

Proof. Clearly, $\mathcal{M}$ is compact by virtue of the Arzelà-Ascoli Theorem. Since moreover for any $\psi \geq 0$, $\psi \not\equiv 0$, we have

$$\begin{aligned}\forall y \in \overline{\Omega}, \quad \mathcal{M}[\psi](y) &= \int_\Omega \mu M(y,z) \frac{\psi(z)}{\sup a - a(z)} dz \\ &\geq \mu m_0 \int_\Omega \frac{\psi(z)}{\sup a - a(z)} dz > 0,\end{aligned}$$

$\mathcal{M}$ satisfies the hypotheses of the Krein-Rutman Theorem 5.6.7, which ensures the well-definition and positiveness of γ_1.

We divide the rest of the proof in two steps:

Step 1: Existence of a solution to (5.3).

We build upon the following remark: if $\mathcal{M}[\Phi] = \gamma_1 \Phi$, then, for $\varphi(y) := \frac{\Phi(y)}{\sup a - a(y)}$, we have

$$\mu M \star \varphi - \big((\sup a - \mu) - (a(y) - \mu)\big)\varphi = (\gamma_1 - 1)\Phi.$$

1. Assume that $\gamma_1 > 1$. Then for $\delta > 0$, we define the regularized operator acting on $\psi \in C_b(\Omega)$:

$$\mathcal{M}^\delta[\psi] = \int_\Omega \mu M(y,z) \frac{\psi(z)}{\delta + \sup a - a(z)} dz.$$

Clearly, $\mathcal{M}^\delta$ is still compact and order-preserving, so that the Krein-Rutman Theorem ensures the existence and uniqueness of a positive eigenpair ($\gamma_1^\delta > 0, \Phi^\delta > 0$) satisfying $\mathcal{M}^\delta[\Phi^\delta] = \gamma_1^\delta \Phi^\delta$. Then we have:

$$\gamma_1^0 = \gamma_1 > 1 \qquad \lim_{\delta\to\infty} \gamma_1^\delta = 0 < 1$$

and thus by continuity of the function $\delta \mapsto \gamma_1^\delta$, there exists $\delta > 0$ such that $\gamma_1^\delta = 1$. Then $\varphi^\delta(y) := \frac{\Phi^\delta(y)}{\delta + \sup a - a(y)}$ satisfies:

$$\mu M \star \varphi^\delta + (a(y) - (\sup a + \delta))\varphi^\delta = (\gamma_1^\delta - 1)\Phi^\delta = 0,$$

which we can rewrite

$$\mu(M \star \varphi^\delta - \varphi^\delta) + \big(a(y) - (\sup a - \mu + \delta)\big)\varphi^\delta = 0.$$

Thus φ^δ is a classical solution to (5.3). Moreover, in this case thanks to Theorem 5.6.3, we have $\lambda_1 < -(\sup a - \mu)$. This shows the direct implication in point (i).

2. Assume $\gamma_1 = 1$. Then $\varphi(y) := \frac{\Phi(y)}{\sup a - a(y)}$ satisfies

$$\mu M \star \varphi + (a(y) - \sup a)\varphi = (\gamma_1 - 1)\Phi = 0.$$

Thus φ is a solution to (5.3) with $\lambda = -(\sup a - \mu)$. This shows the existence in point (ii).

3. Assume now $\gamma_1 < 1$, then the construction from [61] applies, and for any nonnegative nontrivial $\varphi_s \in M^1(\Omega_0)$ there exists a corresponding $\varphi_{ac} \in L^1(\Omega)$, such that $\varphi := \varphi_{ac}dy + \varphi_s$ is a weak solution to (5.3) with $\lambda = -(\sup a - \mu)$. This shows the existence in point (iii).

Step 2: Uniqueness of λ.

Let us show uniqueness. Let $\varphi \in M^1(\overline{\Omega})$ be a nonnegative nontrivial Radon measure solution to (5.3). Then thanks to the Lebesgue-Radon-Nikodym Theorem [184, Theorem 6.10], there exist a nonnegative $\varphi_{ac} \in L^1(\Omega)$ and a nonnegative measure φ_s which is singular with respect to the Lebesgue measure on Ω, such that:

$$\varphi = \varphi_{ac}dy + \varphi_s.$$

It is clear that:

$$(M \star \varphi)(y) = \int_{\overline{\Omega}} M(y,z)\varphi(dz)$$

is a positive and continuous function. Moreover φ satisfies:

$$\forall \psi \in C_b(\overline{\Omega}), \int_{\overline{\Omega}} \mu(M \star \varphi)(y)\psi(y)dy + \int_{\overline{\Omega}} (a(y) - \mu + \lambda)\psi(y)\varphi(dy) = 0,$$

so that

$$\forall \psi \in C_b(\overline{\Omega}), \int_{\overline{\Omega}} \mu(M \star \varphi)(y)\psi(y)dy + \int_{\overline{\Omega}} (a(y) - \mu + \lambda)\psi(y)\varphi_{ac}(y)dy$$
$$= -\int_{\overline{\Omega}} (a(y) - \mu + \lambda)\psi(y)\varphi_s(dy).$$

Since φ_s and the Lebesgue measure are mutually singular $\varphi_s \perp dy$, the above equation is equivalent to the following system:

$$\begin{cases} \mu M \star \varphi_{ac} + (a(y) - \mu + \lambda)\varphi_{ac} = -\mu M \star \varphi_s & a.e.(dy) \\ a(y) - \mu + \lambda = 0 & a.e.(\varphi_s). \end{cases} \tag{5.9}$$

This readily shows that $(a(y)-\mu+\lambda)\varphi_{ac} = -\mu M\star\varphi$ is a continuous negative function and in particular

$$\lambda \leq -(\sup a - \mu).$$

We now distinguish two subcases:

1. Assume $\lambda < -(\sup a - \mu)$. Then the second line of equation (5.9) cannot hold unless $\varphi_s \equiv 0$. Moreover, $\varphi_{ac}(y) = \frac{\mu(M\star\varphi)(y)}{-\lambda-(a(y)-\mu)}$ is then a positive bounded continuous function and satisfies:

$$\mu(M \star \varphi_{ac} - \varphi_{ac}) + (a(y) + \lambda)\varphi_{ac} = 0$$

in the classical sense.

Moreover, we have

$$\mu M \star \varphi_{ac} = (-\lambda + \mu - a(y))\varphi_{ac} > (\sup a - a(y))\varphi_{ac}$$

so that, if we let $\Psi(y) := \varphi_{ac}(y)(\sup a - a(y))$, we have

$$\mathcal{M}[\Psi] = \mu M \star \varphi_{ac} > (\sup a - a)\varphi_{ac} = \Psi$$

which shows, by a classical comparison argument, that $\gamma_1 > 1$.

Now we show that $\lambda = \lambda_1$. Let $(\overline{\lambda}, \overline{\varphi}) \in \mathbb{R} \times C_b(\Omega)$ be such that $\overline{\varphi}(y) > 0$ for $y \in \overline{\Omega}$ and and $\overline{\varphi}$ is a supersolution to (5.3), i.e.

$$\mu M \star \overline{\varphi} + \overline{\varphi}(a(y) - \mu + \overline{\lambda}) \leq 0.$$

Then $\overline{\varphi}(0)(-a(0) - \mu - \overline{\lambda}) \geq \mu M \star \overline{\varphi} > 0$ and thus $\overline{\lambda} < -(a(0) - \mu) = -(\sup a - \mu)$. Since $\overline{\varphi}$ is positive on $\overline{\Omega}$, the number

$$\alpha := \sup\{\zeta > 0, \forall y \in \overline{\Omega}, \zeta\varphi_{ac}(y) \leq \overline{\varphi}(y)\}$$

is well-defined and positive. By definition of α we have $\alpha\varphi_{ac}(y) \leq \overline{\varphi}(y)$ for any $y \in \overline{\Omega}$, and there exists $y_0 \in \overline{\Omega}$ such that $\alpha\varphi_{ac}(y_0) = \overline{\varphi}(y_0)$. We have then

$$\begin{aligned} 0 \leq \mu \int_{\overline{\Omega}} M(y_0, z)\big(\overline{\varphi}(z) - \alpha\varphi_{ac}(z)\big)dz + \big(\overline{\varphi}(y_0) - \alpha\varphi_{ac}(y_0)\big)(a(y_0) - \mu + \overline{\lambda}) \\ \leq 0 - \alpha(\overline{\lambda} - \lambda)\varphi_{ac}(y_0). \end{aligned}$$

Thus $\overline{\lambda} \leq \lambda$. We have shown

$$\lambda \geq \sup\{\overline{\lambda}, \exists \psi \in C_b(\Omega), \psi > 0 \text{ s.t. } \mu(M \star \psi - \psi) + \psi(a(y) + \overline{\lambda}) \leq 0\} = \lambda_1.$$

The reverse inequality $\lambda \leq \lambda_1$ is clear since φ_{ac} is a supersolution to (5.3). Thus $\lambda = \lambda_1$.

This finishes the proof of point (i).

2. On the other hand, assume $\lambda = -(\sup a - \mu)$. We then define $\Psi(y) := \varphi_{ac}(y)(\sup a - a(y)) = \mu(M \star \varphi)$. Then Ψ is a nontrivial positive bounded continuous function which satisfies:

$$\mathcal{M}[\Psi] - \Psi = \mu(M \star \varphi_{ac} - \varphi_{ac}) + (a(y) + \lambda)\varphi_{ac} = -\mu M \star \varphi_s \leq 0.$$

Thus, by a classical comparison argument, $\gamma_1 \leq 1$.

We claim that $\lambda_1 = \lambda$. Indeed, assume by contradiction that $\lambda_1 < \lambda$. By the existence property 5.6.3, there exists then a continuous function $\varphi_1 > 0$ associated with λ_1. Since $\lambda_1 < \lambda = -(\sup a - \mu)$, point 1 above then applies to (λ_1, φ_1) and we have $\gamma_1 > 1$. This is a contradiction. Hence $\lambda = \lambda_1$.

We now distinguish two subcases:

- Assume first $\varphi_s = 0$. Then $\Psi(y) = (\sup a - a(y))\varphi_{ac}(y)$ actually satisfies:

  $$\mathcal{M}[\Psi] - \Psi = \mu M \star \varphi_{ac} - (\sup a - a)\varphi_{ac} = -\mu M \star \varphi_s = 0$$

  and thus $\gamma_1 = 1$. By simplicity of γ_1 as the first eigenvalue of $\mathcal{M}$ given by the Krein-Rutman Theorem, $\varphi \equiv \varphi_{ac}$ is then a multiple of $\frac{\Phi(y)}{\sup a - a(y)}$.

  This finishes the proof of point (ii).

- Assume on the contrary that $\varphi_s \not\equiv 0$. Let $\Psi(y) = (\sup a - a(y))\varphi_{ac}(y)$, then

  $$\mathcal{M}[\Psi] - \Psi = -\mu M \star \varphi_s < 0$$

  and thus $\gamma_1 < 1$. Notice that in this case, the second line in equation (5.9) implies by definition

  $$\varphi_s\left(\{y \in \overline{\Omega}, a(y) \neq \sup a\}\right) = 0$$

  which means supp $\varphi_s \subset \Omega_0$.

  This finishes the proof of point (iii).

In any case, we have shown that if $(\lambda, \varphi) \in \mathbb{R} \times M^1(\overline{\Omega})$ is a weak solution in the sense of measures to (5.3), then $\lambda = \lambda_1$. This finishes the proof of Theorem 5.3.1. □

Below we relax Assumption 5.2.3 to Assumption 5.2.2 but can still prove the uniqueness of a solution to (5.3).

Proposition 5.3.2 (Uniqueness of the solution to (5.3) in the general case)**.** *Let Assumption 5.2.2 hold. Then, there exists a unique λ such that* (5.3) *admits a Radon measure solution, and*

$$\lambda = \lambda_1.$$

Proof. From Theorem 5.3.1, we only need to deal with the complement of Assumption 5.2.3, namely

$$y \mapsto \frac{1}{\sup a - a(y)} \notin L^1(\Omega).$$

In this case, thanks to Theorem 5.6.2 and Theorem 5.6.3, there exists a bounded continuous eigenfunction $\varphi_1 > 0$ associated with λ_1 and $\lambda_1 < -(\sup a - \mu)$.

Let $(\lambda, \varphi) \in \mathbb{R} \times M^1(\overline{\Omega})$ be a solution to (5.3) in the sense of measures. Let us write $\varphi = \varphi_{ac} dy + \varphi_s$, where $\varphi_{ac} \in L^1(\Omega)$. As we did in the proof of Theorem 5.3.1, we rewrite equation (5.3) as:

$$\begin{cases} \mu M \star \varphi_{ac} + (a(y) - \mu + \lambda)\varphi_{ac} = -\mu M \star \varphi_s & a.e.(dy) \\ a(y) - \mu + \lambda = 0 & a.e.(\varphi_s). \end{cases} \tag{5.10}$$

The first line of (5.10) implies that $\lambda \leq -(\sup a - \mu)$. We distinguish two cases:

1. Assume first that $\lambda < -(\sup a - \mu)$. Then the second line of (5.10) cannot hold unless $\varphi_s \equiv 0$. In this case we have $\varphi_{ac}(y) = \frac{\mu M \star \varphi_{ac}(y)}{-\lambda - (a(y) - \mu)}$, which is a positive continuous function. A classical comparison argument then shows $\lambda = \lambda_1$.

2. Assume $\lambda = -(\sup a - \mu)$. Then we can rewrite the first line of (5.10) as:
$$\varphi_{ac}(y) = \frac{\mu M \star \varphi}{\sup a - a(y)}$$
and since $\mu(M \star \varphi)(y) \geq \mu m_0 \int_\Omega \varphi(dz) > 0$, this implies $\varphi_{ac} \notin L^1(\Omega)$, which is a contradiction.

This completes the proof of Proposition 5.3.2. □

5.3.2 The critical mutation rate

In this subsection we investigate further the linear eigenvalue problem (5.3), with $\lambda = \lambda_1$ as compelled by Theorem 5.3.1, under Assumption 5.2.3.

We introduce the notion of *critical mutation rate*, which distinguishes between the existence of a bounded continuous eigenfunction for equation (5.3) and the existence of a singular measure. This is the content of the following theorem:

Theorem 5.3.3 (Critical mutation rate)**.** *Let Assumption 5.2.3 hold. Then, there exists* $\mu_0 = \mu_0(\Omega, M, \sup a - a)$ *such that for any* $0 < \mu < \mu_0$*, problem* (5.3) *has only singular measures solutions with a singularity concentrated in* Ω_0 *(in which case* $\lambda_1 = -(\sup a - \mu)$ *from Theorem 5.3.1), whereas for* $\mu > \mu_0$ *then* (5.3) *has only bounded continuous eigenfunctions.*

Finally, $\mu_0 = \frac{1}{\gamma_1^1}$ *where* γ_1^1 *is the principal eigenvalue of the operator:*

$$\mathcal{M}[\psi] = \int_\Omega M(y,z)\frac{\psi(z)}{\sup a - a(z)}dz$$

acting on bounded continuous functions.

Proof. Let us define, for $\psi \in C_b(\Omega)$,

$$\mathcal{M}^\mu[\psi] = \mu \int_\Omega M(y,z)\frac{\psi(z)}{\sup a - a(z)}dz.$$

Then by the Krein-Rutman Theorem there exists a unique principal eigenpair (γ_1^μ, Φ^μ) satisfying $\gamma_1^\mu > 0$, $\Phi^\mu(y) > 0$, $\sup \Phi^\mu = 1$ and

$$\forall y \in \Omega, \mathcal{M}^\mu[\Phi^\mu] = \gamma_1^\mu \Phi^\mu.$$

Since $\mathcal{M}^\mu = \mu\mathcal{M}^1$, we deduce from the uniqueness of (γ_1^μ, Φ^μ) that

$$\forall \mu > 0, \gamma_1^\mu = \mu\gamma_1^1 \quad \text{and} \quad \Phi^\mu = \Phi^1.$$

The result then follows from the trichotomy in Theorem 5.3.1 □

We can now summarize our findings and prove Proposition 5.2.5:

Proof of Proposition 5.2.5. The first part, under Assumption 5.2.2, follows from Proposition 5.3.2, while the second part, under Assumption 5.2.3, follows from Theorem 5.3.3. □

We prove below that the critical μ_0 is linked to the flatness of the fitness a, which will be used later in the proof of Theorem 5.2.8.

Corollary 5.3.4 (Monotony of μ_0)**.** *Let Assumption 5.2.3 hold and* b *be a continuous function on* $\overline{\Omega}$*, satisfying*

$$\forall y \in \overline{\Omega}, \quad \sup a - a(y) \leq \sup b - b(y).$$

Then we have

$$\mu_0(\Omega, M, \sup a - a) \leq \mu_0(\Omega, M, \sup b - b)$$

where μ_0 *is defined in Theorem 5.3.3.*

Proof. Thanks to our assumptions, we have for $y \in \overline{\Omega}$:

$$0 < \frac{1}{\sup b - b(y)} \leq \frac{1}{\sup a - a(y)}. \tag{5.11}$$

In particular $y \mapsto \frac{1}{\sup b - b(y)} \in L^1(\Omega)$. Thus Theorem 5.3.3 can be applied with both a and b.

We claim that $\gamma_1^b \leq \gamma_1^a$, where γ_1^b, γ_1^a denote the first eigenvalue of the operator $\mathcal{M}_b[\psi] = \int_\Omega M(y,z)\frac{\psi(z)}{\sup b - b(z)}dz$ and $\mathcal{M}_a[\psi] = \int_\Omega M(y,z)\frac{\psi(z)}{\sup a - a(z)}dz$ acting on bounded continuous functions ψ, respectively. Indeed, let $\varphi^a \in C_b(\Omega)$, $\varphi^a > 0$ satisfy $\int_\Omega M(y,z)\frac{\varphi^a(z)}{\sup a - a(z)}dz = \gamma_1^a \varphi^a(y)$ and $\varphi^b \in C_b(\Omega)$, $\varphi^b > 0$ satisfy $\int_\Omega M(y,z)\frac{\varphi^b(z)}{\sup b - b(z)}dz = \gamma_1^b \varphi^b(y)$. Up to multiplication by a positive constant, we assume w.l.o.g. that $\varphi^b \leq \varphi^a$ and that there exists $y \in \overline{\Omega}$ with $\varphi^b(y) = \varphi^a(y) = 1$. At this point, we have

$$\gamma_1^b = \int_\Omega M(y,z)\frac{\varphi^b(z)}{\sup b - b(z)}dz \leq \int_\Omega M(y,z)\frac{\varphi^a(z)}{\sup a - a(z)}dz = \gamma_1^a.$$

We conclude that

$$\mu_0(\Omega, M, \sup a - a) = \frac{1}{\gamma_1^a} \leq \frac{1}{\gamma_1^b} = \mu_0(\Omega, M, \sup b - b)$$

which finishes the proof of Corollary 5.3.4. □

5.3.3 Approximation by a degenerating elliptic eigenvalue problem

Here we show that the previously introduced principal eigenvalue can be approximated by an elliptic Neumann eigenvalue.

Theorem 5.3.5 (Approximating λ_1^ε by regularization)**.** *Let Assumption 5.2.2 hold, and $(\lambda_1^\varepsilon, \varphi^\varepsilon(y) > 0)$ be the solution to the principal eigenproblem:*

$$\begin{cases} -\varepsilon\Delta\varphi^\varepsilon - \mu(M \star \varphi^\varepsilon - \varphi^\varepsilon) = a(y)\varphi^\varepsilon + \lambda_1^\varepsilon \varphi^\varepsilon & \text{in } \Omega \\ \frac{\partial \varphi^\varepsilon}{\partial \nu} = 0 & \text{on } \partial\Omega, \end{cases} \tag{5.12}$$

with $\int_\Omega \varphi^\varepsilon(z)dz = 1$.

Then $\lim_{\varepsilon\to 0} \lambda_1^\varepsilon = \lambda_1$, where λ_1 is the principal eigenvalue defined by (5.2).

Proof. We divide the proof into three steps.

Step 1: We show that λ_1^ε is bounded when $\varepsilon \to 0$.

Integrating equation (5.12) and using the Neumann boundary conditions, we have

$$0 = \int_\Omega (\lambda_1^\varepsilon + a(y))\varphi^\varepsilon dy.$$

The function $a(y)+\lambda_1^\varepsilon$ then has to take nonnegative and nonpositive values. Hence

$$-\sup a \leq \lambda_1^\varepsilon \leq -\inf a.$$

Thus $(\lambda_1^\varepsilon)_{\varepsilon>0}$ is bounded.

Step 2: We identify the limit of converging subsequences.

Let $\lambda_1^{\varepsilon_n}$ be a converging sequence and $\lambda_1^0 := \lim \lambda_1^{\varepsilon_n}$. Then φ^{ε_n} satisfies, for any $\psi \in C^2(\overline{\Omega})$,

$$\int_\Omega -\varepsilon\varphi^{\varepsilon_n}\Delta\psi dy - \varepsilon\int_{\partial\Omega}\varphi^{\varepsilon_n}\frac{\partial\psi}{\partial\nu}dS - \int \mu(M\star\varphi^{\varepsilon_n} - \varphi^{\varepsilon_n})\psi - a(y)\varphi^{\varepsilon_n}\psi \\ = \lambda_1^n\int\varphi^{\varepsilon_n}\psi.$$

In particular, if F_0 denotes the space of functions in $C^2(\Omega)$ with zero boundary flux as in Lemma 5.6.4 item (i), this equation becomes:

$$\int_\Omega -\varepsilon\varphi^{\varepsilon_n}\Delta\psi dy - \int \mu(M\star\varphi^{\varepsilon_n} - \varphi^{\varepsilon_n})\psi - a(y)\varphi^{\varepsilon_n}\psi = \lambda_1^n\int\varphi^{\varepsilon_n}\psi$$

for any $\psi \in F_0$.

Thanks to Prokhorov's Theorem 5.6.9 (that we recalled in Annex 5.6.4), since $\int_\Omega \varphi^{\varepsilon_n}(y)dy = 1$, the sequence $(\varphi^{\varepsilon_n})$ is precompact for the weak topology in $M^1(\overline{\Omega})$, and there exists a weakly convergent subsequence $\varphi^{\varepsilon_n'}$, which converges weakly to a nonnegative Radon measure φ. Since $1 \in C_c(\overline{\Omega})$, we have $\lim\int_{\overline{\Omega}}\varphi^{\varepsilon_n'} = \int_{\overline{\Omega}}\varphi(dy) = 1$. Hence φ is non-trivial. Moreover, we have

$$\mu\int_\Omega\int_\Omega M(y,z)d\varphi(z)\psi(y)dy + \int_\Omega (a(y)-\mu)\psi(y)d\varphi(y) = -\lambda_1^0\int_\Omega\psi(y)d\varphi(y) \tag{5.13}$$

for any test function $\psi \in F_0$. Because F_0 is densely imbedded in $C_b(\overline{\Omega})$ by Lemma 5.6.4, (5.13) holds for any $\psi \in C_b(\overline{\Omega})$. Thanks to Proposition 5.2.5 we have then $\lambda_1^0 = \lambda_1$.

Step 3: Conclusion.

We have shown that for any sequence $\varepsilon_n \to 0$, there exists a subsequence $\varepsilon_n' \to 0$ such that $\lambda_1^{\varepsilon_n'} \to \lambda_1$. Thus $\varepsilon \mapsto \lambda_1^\varepsilon$ when $\varepsilon \to 0$. □

5.4 Stationary states in trait

This section deals with stationary states for (5.1). In particular, we prove Theorem 5.2.6 and Theorem 5.2.8 via a bifurcation argument.

5.4.1 Regularized solutions

We investigate the existence of positive solutions $p = p(y)$ to the following problem

$$\begin{cases} -\varepsilon\Delta p - \mu(M \star p - p) = p(a(y) - K \star p) & \text{in } \Omega \\ \frac{\partial p}{\partial \nu} = 0 & \text{on } \partial\Omega. \end{cases} \tag{5.14}$$

To this end, we actually construct a stationary state for the equation:

$$\begin{cases} -\varepsilon\Delta p - \mu(M \star p - p) = p(a(y) - K \star p - \beta p) & \text{in } \Omega \\ \frac{\partial p}{\partial \nu} = 0 & \text{on } \partial\Omega, \end{cases} \tag{5.15}$$

for any $\beta \geq 0$. Remark that (5.14) is a particular case for (5.15). In particular, in this section we prove the existence of positive solutions for (5.15) when $\lambda_1^\varepsilon < 0$, which also shows the existence of positive solutions for (5.14) when $\lambda_1^\varepsilon < 0$. The reason why we include (5.14) in the more complex situation (5.15) is that solutions to the latter system will be used as subsolutions in the construction of traveling waves in Section 5.5.

Throughout this subsection we denote $(\lambda_1^\varepsilon, \varphi^\varepsilon)$ the eigenpair of the regularized problem, solving (5.12). Notice that $(\lambda_1^\varepsilon, \varphi^\varepsilon)$ is independent from β. Our main result is the following:

Theorem 5.4.1 (Existence of regularized steady states)**.** *Let Assumption 5.2.2 hold, $\varepsilon > 0$ and $(\lambda_1^\varepsilon, \varphi^\varepsilon)$ be defined by* (5.12)*, and $\beta \geq 0$.*

(i) Assume $\lambda_1^\varepsilon > 0$. Then 0 is the only nonnegative solution to (5.15)*.*

(ii) Assume $\lambda_1^\varepsilon < 0$. Then there exists a positive solution to (5.15) *for any $\beta \geq 0$.*

Item (i) is rather trivial and we will discuss it later in the proof of Theorem 5.4.1. The actual construction in the case $\lambda_1^\varepsilon < 0$ is more involved, and we will use the scheme from [7]. We start by establishing *a priori* estimates on the solutions p to (5.15).

Lemma 5.4.2 (*A priori* estimates on p)**.** *Let Assumption 5.2.2 hold, $\varepsilon > 0$, $\beta \geq 0$ and p be a nonnegative nontrivial solution to* (5.15)*. Then:*

(i) p is positive.

(ii) If $\beta = 0$, there exists a positive constant $C = C(\Omega, \varepsilon, \sup a, M, K)$ such that $\|p\|_{L^\infty} \leq C$. If $\beta > 0$ then we have $\sup p \leq \frac{\sup a}{\beta}$.

Proof. Point (i) is trivial thanks to the strong maximum principle at a global minimum. We turn our attention to point (ii).

Assume first $\beta > 0$. Let $y \in \overline{\Omega}$ such that $p(y) = \sup_{z\in\Omega} p(z)$ and assume by contradiction that $p(y) > \frac{\sup a}{\beta}$. If $y \in \Omega$, then we have

$$0 \leq -\varepsilon\Delta_y p(y) - \mu(M \star p - p) = p(a(y) - K \star p - \beta p) < 0$$

which is a contradiction. If $y \in \partial\Omega$, then $\mu(M\star p - p) \leq 0$ and $a - K\star p - \beta p \leq 0$ in a neighbourhood of y, and thus $-\varepsilon\Delta p - (a(y) - K \star p - \beta p)p \leq 0$ in a neighbourhood of y. Thus thanks to Hopf's Lemma we have $\frac{\partial p}{\partial \nu}(y) > 0$, which contradicts the Neumann boundary conditions satisfied by p. Hence $\sup p \leq \frac{\sup a}{\beta}$.

We turn our attention to the case $\beta = 0$, which is more involved. We divide the proof in four steps.

Step 1: We establish a bound on $\int_\Omega p(y)dy$.

Integrating over Ω, we have

$$\int_\Omega a(y)p(y)\mathrm{d}y - \int_\Omega\int_\Omega p(y)K(y,z)p(z)\mathrm{d}y\mathrm{d}z = \beta\int_\Omega p^2(y)dy \geq 0.$$

Thus $\int a(y)p(y)dy \geq k_0 \left(\int_\Omega p(y)dy\right)^2$ and

$$\int_\Omega p(y)dy \leq \frac{\sup a}{k_0}. \tag{5.16}$$

Step 2: We reduce the problem to a boundary estimate.

From Step 1, p is a solution to

$$-\varepsilon\Delta p - (a(y) - \mu - K \star p)p = \mu M \star p$$

where the coefficients and the source term $\mu M\star p$ are bounded independently from p, in the bounded domain Ω. The local maximum principle [108, Theorem 9.20] shows the following property: for any ball $B_{2R}(y) \subset \Omega$, we have

$$\sup_{B_R(y)} p \leq C\left\{\left(\frac{1}{|B_{2R}(y)|}\int_{B_{2R}(y)} p\right) + \mu\frac{R}{\varepsilon}\|M \star p\|_{L^n(B_{2R}(y))}\right\} \tag{5.17}$$

where $C = C(R, \varepsilon, \|a\|_{L^\infty}, k_0, k_\infty, \mu)$. This shows a uniform interior bound $\gamma_R = \gamma_R(C, m_\infty)$ for p (for any point at distance $2R$ from $\partial\Omega$).

To show that this estimate does not degenerate near the boundary, we use a coronation argument. Let $d(y, \partial\Omega) := \inf_{z\in\partial\Omega}|y - z|$, and

$$\Omega_R := \{y \in \Omega, d(y, \partial\Omega) \leq R\}$$

for any $R > 0$. As noted in [91], the function $y \mapsto d(y, \partial\Omega)$ is C^3 on a tubular neighbourhood of $\partial\Omega$. In particular, since $\nabla d \neq 0$ in this neighbourhood, then thanks to the implicit function Theorem, $\partial\Omega_R\backslash\partial\Omega = \{y, d(y, \partial\Omega) = R\}$ is C^3 for $R > 0$ small enough. Moreover, by the comparison principle in narrow domains [27, Proposition 1.1], there exists $\delta > 0$ depending only on Ω, $\|a\|_{L^\infty}$ and ε such that if $|\Omega_R| \leq \delta$, then the maximum principle holds for the operator $-\varepsilon\Delta v - (a(y) - \mu)v$ in Ω_R, meaning that if v satisfies $-\varepsilon\Delta v - (a(y) - \mu)v \geq 0$ in Ω_R and $v \geq 0$ on $\partial\Omega_R$, then $v \geq 0$. In particular, we choose R small enough for this property to hold.

At this point, $p \leq \gamma_R$ in $\Omega\backslash\Omega_R$ and comparison holds in Ω_R.

Step 3: We construct a universal supersolution.

Notice that, in contrast with [5] where Dirichlet boundary conditions are used, we need an additional argument to deal with the Neumann boundary conditions. Since the comparison principle applies in the narrow domain Ω_R, the Fredholm alternative implies that, for any $\delta \in (0, 1]$, there exists a unique (classical) solution to the system:

$$\begin{cases} -\varepsilon\Delta v^\delta - (a(y) - \mu)v^\delta = \mu m_0 \frac{m_\infty \sup a}{k_0} & \text{in } \Omega_R \\ v^\delta = \gamma_R & \text{on } \partial\Omega_R\backslash\partial\Omega \\ \delta v^\delta + (1-\delta)\frac{\partial v^\delta}{\partial\nu} = \delta & \text{on } \ \partial\Omega. \end{cases}$$

Let us remark that thanks to the classical Schauder interior and boundary estimates, the mapping $\delta \mapsto v^\delta$ is actually continuous from $(0, 1]$ to $C_b(\Omega_R)$.

Let us show that v^δ is positive on $\overline{\Omega}$. Thanks to the maximum principle, we have $v^1 \geq 0$. Moreover, the strong maximum principle imposes $v^1 > 0$ in Ω_R. Thus, the quantity

$$\delta_0 := \inf\{\delta \geq 0, \forall y \in \overline{\Omega}_R, \quad v^\delta(y) > 0\}$$

is well-defined and $\delta_0 < 1$. Assume by contradiction that $\delta_0 > 0$. Since v^{δ_0} is the limit of v^δ for $\delta > \delta_0$, then $v^{\delta_0} \geq 0$. Then, there exists $y \in \overline{\Omega}_R$ such that $v^{\delta_0}(y) = 0 = \inf v^{\delta_0}$. Thanks to the strong maximum principle, $y \in \Omega_R$ leads to a contradiction. Since $v^{\delta_0}(z) = \gamma_R > 0$ for $z \in \partial\Omega_R\backslash\partial\Omega$, we have then $y \in \partial\Omega$. Finally, thanks to Hopf's Lemma we have $\frac{\partial v^{\delta_0}}{\partial\nu}(y) < 0$, and thus $\delta v^{\delta_0}(y) + (1-\delta)\frac{\partial v^{\delta_0}}{\partial\nu}(y) < 0$, which is a contradiction. Thus $\delta_0 = 0$. This shows that for any $\delta > 0$, we have $v^\delta > 0$ on $\overline{\Omega}_R$.

Next, thanks to the Schauder estimates, $(v^\delta)_{0<\delta\leq 1}$ is precompact and there exists a sequence $\delta_n \to 0$ and $v \in C^2$ such that $v^{\delta_n} \to v$ in $C^2_{loc}(\Omega_R) \cap C^1(\overline{\Omega}_R)$. Then $v \geq 0$ satisfies:

$$\begin{cases} -\varepsilon\Delta v - (a(y) - \mu)v = \mu m_0 \frac{m_\infty \sup a}{k_0} & \text{in } \Omega_R \\ v = \gamma_R & \text{on } \partial\Omega_R\backslash\partial\Omega \\ \frac{\partial v}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases}$$

Thanks to the strong maximum principle and Hopf's Lemma, we have that $v > 0$ on $\overline{\Omega}_R$.

Step 4: We show that $p \leq v$ on Ω_R.

Let p be a solution to (5.15) and select

$$\eta := \inf\{\zeta > 0, \zeta v \geq p \text{ in } \Omega_R\}.$$

Assume by contradiction that $\eta > 1$. Then there exists $y_0 \in \overline{\Omega}_R$ such that $p(y_0) = \eta v(y_0)$ and $\eta v - p \geq 0$. In particular y_0 is a zero minimum for the function $\eta v - p$. If $y_0 \in \partial\Omega$, then by Hopf's Lemma we have $\frac{\partial(\eta v - p)}{\partial \nu}(y_0) < 0$ which is a contradiction since both p and v satisfy a Neumann boundary value problem. Thus $y_0 \notin \partial\Omega$. Since $\eta > 1$ and $p(z) \leq \gamma_R < \eta\gamma_R = \eta v(z)$ for $z \in \Omega\backslash\Omega_R$, then $y_0 \notin \partial\Omega_R\backslash\partial\Omega$, which shows that $y_0 \in \Omega_R$. Now y_0 is an interior local minimum to $\eta v - p$ and thus

$$\begin{aligned}0 \geq -\varepsilon\Delta(\eta v - p)(y_0) &= (a(y_0) - \mu)(\eta v - p)(y_0) + \eta\mu m_0 \frac{m_\infty \sup a}{k_0} \\ &\quad - \mu(M \star p)(y_0) + p(y_0)(K \star p)(y_0) \\ &> \eta\mu m_0 \frac{m_\infty \sup a}{k_0} - \mu(M \star p)(y_0) \geq 0,\end{aligned}$$

thanks to (5.16),which is a contradiction. Thus $\eta \leq 1$.

This shows that $p \leq v$. Since v is a bounded function, we have our uniform bound for p in Ω_R. In $\Omega\backslash\Omega_R$, thanks to (5.17), we have $p \leq \gamma_R$. This ends the proof of Lemma 5.4.2. □

In order to proceed to the proof of Theorem 5.4.1, we yet need an additional technical remark:

Lemma 5.4.3 (Fréchet differentiability at 0)**.** *Let Assumption 5.2.2 hold,* $\beta \geq 0$ *and*

$$\begin{array}{rccl} G: & C_b(\Omega) & \to & C_b(\Omega) \\ & p(y) & \mapsto & p(y)(K \star p)(y) + \beta p^2(y), \end{array}$$

then G *is Fréchet differentiable at* $p = 0$ *and its derivative is* $DG(p) = 0$.

Proof. Indeed, we have

$$\begin{aligned}\left| \int_\Omega K(y,z)p(z)dz p(y) + p^2(y) \right| &\leq \int_\Omega K(y,z)|p(z)|dz|p(y)| + \beta p^2(y) \\ &\leq k_\infty |\Omega| \|p\|^2_{C_b(\Omega)} + \beta \|p\|^2_{C_b(\Omega)}\end{aligned}$$

which shows that $\|G(p)\|_{C_b(\Omega)} \leq (k_\infty|\Omega| + \beta)\|p\|^2_{C_b(\Omega)} = o\left(\|p\|_{C_b(\Omega)}\right)$. Thus G is Fréchet differentiable with derivative 0 at 0. □

Proof of Theorem 5.4.1. **Step 1:** We prove item (i).

We assume $\lambda_1^\varepsilon > 0$. We recall that $(\lambda_1^\varepsilon, \varphi^\varepsilon)$ is the solution to (5.12) with $\int_\Omega \varphi^\varepsilon(y)dy = 1$. Let $p > 0$ be a nonnegative solution to (5.15) in Ω. Since p is bounded and φ^ε is positive on $\overline{\Omega}$, the quantity

$$\alpha := \inf\{\zeta > 0, \zeta\varphi^\varepsilon > p\}$$

is well-defined and finite. Then, there exists $y \in \overline{\Omega}$ such that $u(y) = \alpha\varphi^\varepsilon(y)$. Remark that y is a minimum to the nonnegative function $\alpha\varphi^\varepsilon - p$. If $y \in \partial\Omega$, then Hopf's Lemma implies $\frac{\partial(\alpha\varphi^\varepsilon - p)}{\partial\nu}(y) < 0$, which contradicts the Neumann boundary conditions satisfied by p and φ^ε. Thus $y \in \Omega$. Evaluating equation (5.15), we have :

$$\begin{aligned}0 \geq -\varepsilon\Delta(\alpha\varphi^\varepsilon - p)(y) &= \mu\big(M \star (\alpha\varphi^\varepsilon - p) - (\alpha\varphi^\varepsilon - p)\big) \\ &\quad + a(y)\big(\alpha\varphi^\varepsilon(y) - p(y)\big) + p(y)(K \star p)(y) + \beta p^2(y) + \lambda_1^\varepsilon \alpha\varphi^\varepsilon \\ &\geq p(y)(K \star p)(y) + \beta p^2(y) + \lambda_1^\varepsilon\alpha\varphi^\varepsilon > 0\end{aligned}$$

which is a contradiction.

Step 2 : We prove item (ii).

We assume $\lambda_1^\varepsilon < 0$. We argue as in [7]: roughly speaking, if the nonlinearity is neglectable near 0 and we can prove local boundeness of the solutions in L^∞, then we can prove existence through a bifurcation argument. This requires topological results that are stated in Appendix 5.6.3.

More precisely, for $\alpha \in \mathbb{R}$ and $p \in C_b(\Omega)$, we let $F(\alpha, p) = \tilde{p}$ where $\tilde{p}$ is the unique solution to:

$$\begin{cases} -\varepsilon\Delta\tilde{p} + (\sup a - a(y))\tilde{p} - \mu(M \star \tilde{p} - \tilde{p}) = \alpha p - G(p) & \text{in } \Omega \\ \frac{\partial\tilde{p}}{\partial\nu} = 0 & \text{on } \partial\Omega \end{cases}$$

where G is as in Lemma 5.4.3. Notice that $\sup a - a(y) \geq 0$, so comparison applies and the operator F is well-defined thanks to the Fredholm alternative. In particular, for each $\alpha \in \mathbb{R}$, $F(\alpha, \cdot)$ is Fréchet differentiable near 0 and its derivative is the linear operator αT, where $Tp = q$ and q is defined by:

$$\begin{cases} -\varepsilon\Delta q + (\sup a - a(y))q - \mu(M \star q - q) = p & \text{in } \Omega \\ \frac{\partial q}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases}$$

Let $C := \{p \in C_b(\Omega), p \geq 0\}$. Let us show that T maps the cone $C\backslash\{0\}$ into $Int\ C = \{p \in C_b(\Omega), p > 0\}$. Assume by contradiction that there is $p \geq 0$, $p \neq 0$ such that $q = Tp$ has a nonpositive global minimum at y. Then if $y \in \partial\Omega$, Hopf's Lemma implies that $\frac{\partial q}{\partial\nu}(y) < 0$, which contradicts the Neumann boundary conditions satisfied by q. Thus $y \in \Omega$. By definition, we have then

$$0 \geq -\varepsilon\Delta q = p(y) + (a(y) - \sup a)q(y) + \mu\left(\int_\Omega M(y,z)(q(z) - q(y))dz\right)$$

which is a contradiction unless q is constant. In the latter case we verify that $q(y) = \frac{p(y)}{\sup a - a(y)}$ is positive. Hence we have a contradiction. We conclude that T maps $C\backslash\{0\}$ into $Int\ C$.

Let us determine the first eigenvalue $\lambda(T)$ of the operator T. A first eigenpair $(\lambda(T), \psi)$ satisfies $T\psi = \lambda(T)\psi$, i.e.

$$\begin{cases} -\varepsilon\Delta\psi + (\sup a - a(y))\psi - \mu(M \star \psi - \psi) = \frac{\psi}{\lambda(T)} & \text{in } \Omega \\ \frac{\partial\psi}{\partial\nu} = 0 & \text{on } \partial\Omega, \end{cases}$$

and equivalently:

$$\begin{cases} -\varepsilon\Delta\psi - \mu(M \star \psi - \psi) = a(y)\psi + \left(\frac{1}{\lambda(T)} - \sup a\right)\psi & \text{in } \Omega \\ \frac{\partial\psi}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases}$$

By the uniqueness in the Krein-Rutman Theorem 5.6.7, we have therefore the identity $\lambda_1^\varepsilon = \frac{1}{\lambda(T)} - \sup a$.

We now verify one by one the hypotheses of Theorem 5.6.8:

1. Clearly we have $F(\alpha, 0) = 0$ for any $\alpha \in \mathbb{R}$.

2. Thanks to Lemma 5.4.3, G is Fréchet differentiable near 0 with derivative 0. As a consequence, $F(\alpha, \cdot)$ is Fréchet differentiable near 0 with derivative αT.

3. T satisfies the hypotheses of Theorem 5.6.7.

4. Item (ii) in Lemma 5.4.2 shows a uniform bound on the eventual solutions to $F(\alpha, p) = p$. More precisely, such a solution satisfies

$$\begin{cases} -\varepsilon\Delta p + (\sup a - a)p - \mu(M \star p - p) = \alpha p - (K \star p + \beta p)p & \text{in } \Omega \\ \frac{\partial p}{\partial\nu} = 0 & \text{on } \partial\Omega, \end{cases}$$

which we can write as

$$\begin{cases} -\varepsilon\Delta p - \mu(M \star p - p) = \big((a(y) - \sup a + \alpha) - (K \star p + \beta p)\big)p & \text{in } \Omega \\ \frac{\partial p}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases}$$

This shows that Lemma 5.4.2 applies.

5. Since any nontrivial nonnegative fixed point p is positive, there is no nontrivial fixed point in the boundary of C.

Thus, applying Theorem 5.6.8, there exists a branch of solutions $\mathcal{C}$ connecting $\alpha = \frac{1}{\lambda(T)}$ to either $\alpha \to +\infty$ or $\alpha \to -\infty$. We remark the principal eigenproblem associated with the equation $F(\alpha, p) = p$ is:

$$\begin{cases} -\varepsilon\Delta\varphi^\alpha - \mu(M \star \varphi^\alpha - \varphi^\alpha) = (a(y) - \sup a + \alpha)\varphi^\alpha + \lambda^\alpha\varphi^\alpha & \text{in } \Omega \\ \frac{\partial\varphi^\varepsilon}{\partial\nu} = 0 & \text{on } \partial\Omega. \end{cases}$$

We can find the principal eigenvalue explicitely: $\lambda^\alpha = \lambda_1^\varepsilon + \sup a - \alpha = \frac{1}{\lambda(T)} - \alpha$. In particular, for $\alpha < -\sup a - \lambda_1^\varepsilon$, we deduce from point (i) in Theorem 5.4.1 (that we proved above) that there cannot exist a solution to $F(\alpha, p) = p$ in C.

We have shown that there exists no nontrivial solution to $F(\alpha, p) = p$ for any $\alpha < \frac{1}{\lambda(T)}$. Thus $\mathcal{C}$ connects $\frac{1}{\lambda(T)}$ to $+\infty$. In particular, there exists a solution for $\alpha = \sup a = \frac{1}{\lambda(T)} - \lambda_1^\varepsilon > \frac{1}{\lambda(T)}$, and such a solution solves (5.15). This ends the proof of Theorem 5.4.1. □

We now prove a lower estimate for solutions to (5.15) that will be crucial for the construction of traveling wave, but will not be used in the meantime. We stress that in the lemma below, the constant ρ_β is independent from ε.

Lemma 5.4.4 ($p^{\varepsilon,\beta}$ does not vanish)**.** *Let Assumption 5.2.2 hold and suppose $\beta > 0$, $\lambda_1 < 0$. Let $p^{\varepsilon,\beta}$ be a solution to* (5.15)*. Then, there exist constants $\varepsilon_0 = \varepsilon_0(\Omega, \mu, M, a) > 0$ and $\rho_\beta = \rho_\beta(\Omega, M, a, \beta) > 0$ such that if $\varepsilon \leq \varepsilon_0$, then*

$$\inf_\Omega p^{\varepsilon,\beta} \geq \rho_\beta.$$

Proof. This proof is inspired by [62].

Step 1: Setting of an approximating eigenvalue problem.

Let $\delta > 0$, $\varepsilon > 0$, $a^\delta(y) := \min(a(y), \sup a - \delta)$ and $(\lambda^{\delta,\varepsilon}, \varphi^{\delta,\varepsilon})$ be the principal eigenpair solving the problem

$$\begin{cases} \varepsilon \Delta \varphi^{\delta,\varepsilon} + \mu(M \star \varphi^{\delta,\varepsilon} - \varphi^{\delta,\varepsilon}) + (a^\delta(y) + \lambda^{\delta,\varepsilon})\varphi^{\delta,\varepsilon} = 0 & \text{in } \Omega \\ \frac{\partial \varphi^{\delta,\varepsilon}}{\partial \nu} = 0 & \text{on } \partial\Omega, \end{cases} \tag{5.18}$$

with $\int_\Omega \varphi^{\delta,\varepsilon}(y)dy = 1$. It follows from Theorem 5.3.5 that $\lambda^{\delta,\varepsilon}$ converges to the principal eigenvalue $\lambda^{\delta,0}$ of the operator $\psi \mapsto \mu(M \star \psi - \psi) + a^\delta(y)\psi$ when $\varepsilon \to 0$. $\lambda^{\delta,0}$, in turn, converges to λ_1 when $\delta \to 0$ by the Lipschitz continuity in Theorem 5.6.1. Thus we may approximate λ_1 by $\lambda^{\delta,\varepsilon}$ for $\delta > 0$ and $\varepsilon > 0$ small enough.

Since $y \mapsto \frac{1}{\sup a^\delta - a^\delta(y)} \notin L^1(\Omega)$, it follows from Theorem 5.6.2 that there exists a continuous eigenfunction associated with $\lambda^{\delta,0}$. In this case Theorem 5.6.3 shows the strict bound $\lambda^{\delta,0} < -\sup a^\delta + \mu = -\sup a + \delta + \mu$.

In what follows we fix $\delta > 0$ so that $\delta < \min\left(\mu, \frac{1}{2}(\sup a - \inf a)\right)$ and $\lambda^{\delta,0} \leq \frac{3\lambda_1}{4}$. We let $\eta := -\lambda^{\delta,0} - \sup a + \delta + \mu > 0$. Since $\lambda^{\delta,\varepsilon} \to \lambda^{\delta,0}$ as $\varepsilon \to 0$, we fix $\varepsilon_0 > 0$ such that for any $0 < \varepsilon < \varepsilon_0$, $|\lambda^{\delta,\varepsilon} - \lambda^{\delta,0}| \leq \frac{-\lambda_1}{4}$ and $\lambda^{\delta,\varepsilon} \leq \lambda^{\delta,0} + \frac{\eta}{2}$.

Finally, integrating equation (5.18) over Ω, we have

$$0 = \int_\Omega (a^\delta(y) + \lambda^{\delta,\varepsilon})\varphi^{\delta,\varepsilon}(y)dy,$$

thus the function $a^\delta(y) + \lambda^{\delta,\varepsilon}$ takes nonpositive and nonnegative values, which shows

$$\inf a = \inf a^\delta \leq \lambda^{\delta,\varepsilon} \leq \sup a^\delta = \sup a - \delta.$$

Step 2: Estimates from above and from below of $\varphi^{\delta,\varepsilon}$.

Let us establish some upper and lower bounds for $\varphi^{\delta,\varepsilon}$. First, there exists $y \in \overline{\Omega}$ such that $\varphi^{\delta,\varepsilon}(y) = \inf_{z\in\overline{\Omega}} \varphi^{\delta,\varepsilon}(z)$. If $y \in \partial\Omega$, then thanks to Hopf's Lemma we have $\frac{\partial\varphi^{\delta,\varepsilon}}{\partial\nu}(y) < 0$, which contradicts the Neumann boundary conditions satisfied by $\varphi^{\delta,\varepsilon}$. We conclude that $y \in \Omega$. Thus we can evaluate equation (5.18):

$$0 \geq -\varepsilon\Delta\varphi^{\delta,\varepsilon}(y) = \mu\left(M \star \varphi^{\delta,\varepsilon} - \varphi^{\delta,\varepsilon}\right) + (a^\delta(y) + \gamma)\varphi^{\delta,\varepsilon},$$

$$(\sup a - \inf a)\varphi^{\delta,\varepsilon}(y) \geq (-\lambda^{\delta,\varepsilon} - a^\delta(y_0) + \mu)\varphi^{\delta,\varepsilon}(y_0) \geq \mu m_0 \int_\Omega \varphi^{\delta,\varepsilon} = \mu m_0,$$

and we arrive at

$$\min_{z\in\Omega} \varphi^{\delta,\varepsilon}(z) \geq \frac{\mu m_0}{\sup a - \inf a}.$$

Similarily, there exists $y \in \Omega$ such that $\varphi^{\delta,\varepsilon}(y) = \max_{z\in\Omega}\varphi^{\delta,\varepsilon}(z)$. Evaluating equation (5.18), we get:

$$0 \leq -\varepsilon\Delta\varphi^{\delta,\varepsilon} = \mu M \star \varphi^{\delta,\varepsilon} + (b(y) - \mu + \lambda^{\delta,\varepsilon})\varphi^{\delta,\varepsilon}(y),$$

and since $a^\delta(y) - \mu + \lambda^{\delta,\varepsilon} \leq -\frac{\eta}{2} < 0$, we have:

$$\frac{\eta}{2}\varphi^{\delta,\varepsilon} \leq \mu m_\infty \int_\Omega \varphi^{\delta,\varepsilon} = \mu m_\infty,$$

and thus

$$\max_{z\in\Omega} \varphi^{\delta,\varepsilon}(z) \leq 2\frac{\mu m_\infty}{\eta}.$$

In other words, φ is uniformly bounded from above and from below when $\varepsilon \to 0$: for $0 < \varepsilon \leq \varepsilon_0$ and $y \in \Omega$, we have shown that

$$\frac{\mu m_0}{\sup a - \inf a} \leq \varphi^{\delta,\varepsilon}(y) \leq 2\frac{\mu m_\infty}{\eta}.$$

Step 3: Lower estimate for $p^{\varepsilon,\beta}$.

We are now in position to derive a lower bound for $p^{\varepsilon,\beta}$. Let $p := p^{\beta,\varepsilon}$ be a solution to (5.15) with $\beta \geq 0$. Since $p^{\varepsilon,\beta} > 0$ in Ω, we can define

$$\alpha := \sup\{\zeta > 0, \forall y \in \Omega, \zeta\varphi^{\delta,\varepsilon}(y) \leq p^{\varepsilon,\beta}(y)\}.$$

Assume by contradiction that $\alpha < \alpha_0 := \min\left(\frac{m_0\eta}{2k_\infty m_\infty}, \frac{-\lambda^{\delta,\varepsilon}\eta}{2\beta\mu m_\infty + \eta k_\infty}\right)$. Then we have

$$\forall y \in \Omega, \mu M(y,z) - \alpha\varphi^{\delta,\varepsilon}(y)K(y,z) \geq \mu m_0 - k_\infty\frac{m_0\eta}{2k_\infty m_\infty}\frac{2\mu m_\infty}{\eta} = 0.$$

By definition of α there exists $y \in \overline{\Omega}$ such that $\alpha\varphi^{\delta,\varepsilon}(y) = p(y)$. Assume $y \in \partial\Omega$, then thanks to Hopf's Lemma we have $\frac{\partial(p^{\varepsilon,\beta} - \varphi^{\delta,\varepsilon})}{\partial\nu}(y) < 0$, which contradicts the Neumann boundary conditions satisfied by $p^{\varepsilon,\beta}$ and $\varphi^{\delta,\varepsilon}$. Thus $y \in \Omega$. We have:

$$\begin{aligned}
0 \geq -\varepsilon\Delta(p^{\varepsilon,\beta} - \alpha\varphi^{\delta,\varepsilon})(y) &= \mu\left(M \star (p^{\varepsilon,\beta} - \alpha\varphi^{\delta,\varepsilon}) - (p^{\varepsilon,\beta} - \varphi^{\delta,\varepsilon})\right) \\
&\quad + p^{\varepsilon,\beta}(a(y) - K \star p^{\varepsilon,\beta} - \beta p^{\varepsilon,\beta}) - (\lambda^{\delta,\varepsilon} + a^{\delta}(y))\alpha\varphi^{\delta,\varepsilon} \\
&= \int_\Omega (\mu M(y,z) - \alpha\varphi^{\delta,\varepsilon}(y)K(y,z))(p^{\varepsilon,\beta}(z) - \alpha\varphi^{\delta,\varepsilon}(z))dz \\
&\quad - \alpha\varphi^{\delta,\varepsilon}(y)\int_\Omega K(y,z)(\alpha\varphi^{\delta,\varepsilon}(z))dz \\
&\quad + \alpha\varphi^{\delta,\varepsilon}(a(y) - a^{\delta}(y)) - \beta\left(p^{\varepsilon,\beta}\right)^2 - \lambda^{\delta,\varepsilon}\alpha\varphi^{\delta,\varepsilon}(y).
\end{aligned}$$

By the former remark, $\mu M(y,z) - \alpha\varphi^{\delta,\varepsilon}(y)K(y,z) \geq 0$ and thus since $p^{\varepsilon,\beta}(y) = \alpha\varphi^{\delta,\varepsilon}(y)$ and $a(y) \geq a^{\delta}(y)$,

$$0 \geq -\alpha\lambda^{\delta,\varepsilon}\varphi^{\delta,\varepsilon}(y) - \alpha^2\varphi^{\delta,\varepsilon}(y)\left(\beta\varphi^{\delta,\varepsilon} + \int_\Omega K(y,z)\varphi^{\delta,\varepsilon}(z)dz\right)$$

which we write

$$(2\beta\frac{\mu m_\infty}{\eta} + k_\infty)\alpha \geq \alpha\left(\beta\varphi^{\delta,\varepsilon}(y) + \int_\Omega K(y,z)\varphi^{\delta,\varepsilon}(z)dz\right) \geq -\lambda^{\delta,\varepsilon},$$

which is a contradiction since $\alpha < \alpha_0 = \min\left(\frac{m_0\eta}{2k_\infty m_\infty}, \frac{-\lambda^{\delta,\varepsilon}\eta}{2\beta\mu m_\infty + \eta k_\infty}\right)$.

We conclude that $\alpha \geq \alpha_0$ and thus

$$\begin{aligned}
\min_{y\in\Omega} p^{\varepsilon,\beta}(y) &\geq \alpha_0 \min_{y\in\Omega}\varphi^{\delta,\varepsilon}(y) \\
&\geq \min\left(\frac{m_0\eta}{2k_\infty m_\infty}, \frac{-\lambda^{\delta,\varepsilon}\eta}{2\beta\mu m_\infty + \eta k_\infty}\right)\frac{\mu m_0}{\sup a - \inf a},
\end{aligned}$$

and since $\lambda^{\delta,\varepsilon} \leq \frac{\lambda_1}{2}$,

$$\min_{y\in\Omega} p^{\varepsilon,\beta}(y) \geq \min\left(\frac{m_0\eta}{2k_\infty m_\infty}, \frac{(-\lambda_1)\eta}{4\beta\mu m_\infty + 2\eta k_\infty}\right)\frac{\mu m_0}{\sup a - \inf a} > 0.$$

Since the lower bound is independent from ε, this ends the proof of Lemma 5.4.4. □

5.4.2 Construction of a stationary solution at $\varepsilon = 0$

Since $\lambda_1^\varepsilon \to \lambda_1$ when $\varepsilon \to 0$, if $\lambda_1 < 0$ then for $\varepsilon > 0$ small enough Theorem 5.4.1 guarantees the existence of a positive solution to (5.15). Notice that this holds in particular for $\beta = 0$, which gives us the existence of a solution to (5.14).

When $\varepsilon \to 0$, we expect the constructed solution to converge weakly to a (possibly singular) Radon measure. Here we prove this result, which will complete Theorem 5.2.6. In particular, in this subsection we are only concerned with the case $\beta = 0$.

Before we can prove theorem 5.2.6, we need a series of estimates on the previously constructed solutions p^ε.

Lemma 5.4.5 (Estimates on the mass)**.** *Let Assumption 5.2.2 hold, $\varepsilon > 0$ such that $\lambda_1^\varepsilon < 0$, and p^ε be a solution to equation* (5.14)*. Then*

$$\frac{-\lambda_1^\varepsilon}{k_\infty} \leq \int_\Omega p^\varepsilon(y)dy \leq \frac{\sup a}{k_0}.$$

In particular, $\int p^\varepsilon$ is bounded from above and from below by positive constants when $\varepsilon \to 0$.

Proof. **Lower bound :** Let $\varphi^\varepsilon > 0$ satisfy equation (5.12) and $\int \varphi^\varepsilon = 1$. Since $p^\varepsilon > 0$ and φ^ε is bounded, we can define

$$\alpha := \sup\{\zeta > 0, \forall y \in \Omega, \zeta\varphi^\varepsilon \leq p^\varepsilon\} > 0.$$

By definition of α we have $\alpha\varphi^\varepsilon \leq p^\varepsilon$ and there exists $y \in \overline{\Omega}$ such that $p^\varepsilon(y) = \alpha\varphi^\varepsilon(y)$. If $y \in \partial\Omega$, since y is a maximum point for the function $\alpha\varphi^\varepsilon - p^\varepsilon$, then thanks to Hopf's Lemma we have $\frac{\partial \alpha\varphi^\varepsilon - p^\varepsilon}{\partial\nu}(y) > 0$, which contradicts the Neumann boundary conditions satisfied by p^ε and φ^ε. Thus $y \in \Omega$ and we compute

$$\begin{aligned} 0 &\leq -\mu\big(M \star (\alpha\varphi^\varepsilon - p^\varepsilon) - (\alpha\varphi^\varepsilon - p^\varepsilon)\big) - \varepsilon\Delta(\alpha\varphi^\varepsilon - p^\varepsilon) - a(y)(\alpha\varphi^\varepsilon - p^\varepsilon) \\ &= \lambda_1^\varepsilon\alpha\varphi^\varepsilon + (K \star p^\varepsilon)p^\varepsilon, \end{aligned}$$

so that

$$\big(\lambda_1^\varepsilon + (K \star p^\varepsilon)(y)\big)p^\varepsilon(y) \geq 0,$$

and thus

$$k_\infty \int_\Omega p^\varepsilon(z)dz \geq (K \star p^\varepsilon)(y) \geq -\lambda_1^\varepsilon.$$

Upper bound : Integrating over Ω, we get

$$0 = \int_\Omega \big(a(y) - (K \star p^\varepsilon)(y)\big)p^\varepsilon(y)dy,$$

$$\begin{aligned} k_0 \left(\int_\Omega p^\varepsilon(y)dy\right)^2 &\leq \iint_{\Omega\times\Omega} K(y,z)p^\varepsilon(z)p^\varepsilon(y)dzdy = \int_\Omega a(y)p^\varepsilon(y)dy \\ &\leq \sup a \int_\Omega p^\varepsilon(y)dy, \end{aligned}$$

which shows the upper bound. ☐

Proof of Theorem 5.2.6. Thanks to Lemma 5.4.5, the family $(p^\varepsilon)_{0<\varepsilon\leq 1}$ of solutions to (5.14) with $\varepsilon > 0$ is uniformly bounded in $M^1(\overline{\Omega})$. Thanks to Prokhorov's Theorem 5.6.9, $(p^\varepsilon)_{0<\varepsilon<1}$ is precompact for the weak topology in $M^1(\overline{\Omega})$, and thus there exists a sequence p^{ε_n} (with $\varepsilon_n \to 0$) and a measure p such that $p^{\varepsilon_n} \rightharpoonup p$ in the sense of measures, i.e.

$$\forall \psi \in C_b(\overline{\Omega}), \quad \lim_{n\to\infty} \int_\Omega \psi(y) p^{\varepsilon_n}(y)dy = \int_{\overline{\Omega}} \psi(y)p(dy).$$

In particular, taking $\psi = 1$, we recover thanks to Lemma 5.4.5:

$$0 < \frac{-\lambda_1}{k_\infty} \leq \int_{\overline{\Omega}} p(dy) \leq \frac{\sup a}{k_0}.$$

Hence p is non-trivial.

Let us show that p is a solution to (5.4). Let F_0 be the space of all functions $\psi \in C^2(\overline{\Omega})$ which satisfy $\frac{\partial \psi}{\partial \nu} = 0$ on $\partial\Omega$, as in Lemma 5.6.4 item (i). Then, multiplying equation (5.14) by ψ and integrating, we get

$$-\varepsilon \int_\Omega p^{\varepsilon_n} \Delta\psi dy = \int_\Omega \mu(M\star p^{\varepsilon_n} - p^{\varepsilon_n})\psi + a(y)p^{\varepsilon_n}\psi dy - \int_\Omega (K\star p)(y)\psi(y)p(y)dy. \tag{5.19}$$

Since $\Delta\psi$ is a bounded continuous function over Ω and $\int_\Omega p^{\varepsilon_n}$ is bounded uniformly in ε, the left-hand side of (5.19) goes to 0 when $n \to \infty$. Moreover since $\psi(y)(a(y) - \mu)$ is a bounded continuous functions, then by definition

$$\int_\Omega \psi(y)(a(y) - \mu)p^{\varepsilon_n}(y)dy \to_{n\to\infty} \int_{\overline{\Omega}} \psi(y)(a(y) - \mu)p(dy).$$

We turn our attention to the term $\int_\Omega M \star p^{\varepsilon_n}(y)\psi(y)dy$. We notice that

$$\begin{aligned}\left|(M \star p^{\varepsilon_n})(y) - (M \star p^{\varepsilon_n})(y')\right| =& \left|\int_\Omega \big(M(y,z) - M(y',z)\big)p^{\varepsilon_n}(z)dz\right| \\ \leq& 2\|M(y,\cdot) - M(y,\cdot)\|_{C_b(\Omega)} \frac{\sup a}{k_0}.\end{aligned}$$

Thus, since M is uniformly continuous over the compact set $\overline{\Omega} \times \overline{\Omega}$, the modulus of continuity of $M \star p^{\varepsilon_n}$ is uniformly bounded. Up to the extraction of a subsequence (independent from ψ), $M \star p^{\varepsilon_n}$ therefore converges in $C_b(\Omega)$ to $M \star p$. Along this subsequence (that we will still denote ε_n for the rest of the proof), we have therefore

$$\lim_{n\to\infty} \int_\Omega (M \star p^{\varepsilon_n})(y)\psi(y)dy = \int_\Omega (M \star p)\psi(y)dy.$$

Likewise, up to the extraction of a subsequence (independent from ψ), the function $K \star p^{\varepsilon_n}$ converges uniformly to $K \star p$, and therefore

$$\lim_{n\to\infty} \int_\Omega (K \star p^{\varepsilon_n})(y)\psi(y)p^{\varepsilon_n}(y)dy = \int_\Omega (K \star p)\psi(y)p(dy).$$

We have shown that equation (5.19) is satisfied for any $\psi \in F_0$. Thanks to Lemma 5.6.4, F_0 is densely imbedded in $C_b(\overline{\Omega})$. Equation (5.19) is thus satisfied for any $\psi \in C_b(\overline{\Omega})$. This ends the proof of Theorem 5.2.6. $\square$

5.4.3 Existence of a singular measure when the trait 0 is dominant

Under Assumption 5.2.7 and if μ is small enough ($\mu < \mu_0$), we can actually prove that the measure solution to (5.4) is concentrated in Ω_0 (Theorem 5.2.8). The sketch of the proof is to write a solution p to (5.4) as an eigenvector for a problem similar to (5.3), and make use of Theorem 5.3.1.

Proof of Theorem 5.2.8. Let p be a nonnegative nontrivial measure solution to (5.4). Define $b(y) := a(y) - (K \star p)(y)$. Then b is a continuous function and we have for $y \in \overline{\Omega}$:

$$b(y) = a(y) - \int_{\overline{\Omega}} K(y,z)p(dz) \le a(0) - \int_{\overline{\Omega}} K(0,z)p(dz) = b(0)$$

thanks to Assumption 5.2.7. This shows that $\sup b = b(0)$. Next we compute:

$$b(0) - b(y) = a(0) - a(y) + \int_{\overline{\Omega}} \big(K(y,z) - K(0,z)\big)p(dz) \ge a(0) - a(y),$$

where we have again used Assumption 5.2.7. Thus, b satisfies Assumption 5.2.3.

We remark that p solves

$$\mu(M \star p - p) + b(y)p = 0 \tag{5.20}$$

in the sense of measures. Thus p is a solution to (5.3) with a replaced by b. Applying Corollary 5.3.4, since $\mu < \mu_0(\Omega, M, \sup a - a)$, then $\mu < \mu_0(\Omega, M, \sup b - b)$ and thus the only solutions to (5.20) are singular measures which singular part is concentrated in $\{y \in \Omega, b(y) = \sup b\}$. Let us show that $\{y, b(y) = \sup b\} \subset \Omega_0$. Let $y \in \overline{\Omega}$ such that $y \notin \Omega_0$. Then $a(y) < a(0)$ and

$$b(y) = a(y) - (K \star p)(y) < a(0) - (K \star p)(y) \le a(0) - (K \star p)(0) = \sup b,$$

which shows that $y \notin \{y, b(y) = \sup b\}$. This ends the proof of Theorem 5.2.8. $\square$

5.5 Construction of traveling waves

In this section, we prove our main result Theorem 5.2.10. To construct the desired measure traveling wave, we first consider a regularized problem in a box $-l \leq x \leq l$, $y \in \Omega$.

5.5.1 Construction of a solution in a box

Here we aim at constructing solutions $(c, u = u(x,y))$ to

$$\begin{cases} -\varepsilon\Delta_y u - u_{xx} - cu_x = \mu(M \star u - u) & \\ \qquad\qquad\qquad\qquad +u(a(y) - K \star u) & \text{in } (-l,l) \times \Omega \\ \nabla_y u(x,y) \cdot \nu = 0 & \text{on } (-l,l) \times \partial\Omega \\ u(l,y) = 0 & \text{in } \Omega \\ u(-l,y) = p(y) & \text{in } \Omega, \end{cases} \tag{5.21}$$

where $p(y)$ is the previously constructed stationary state, solving (5.14). To this end we investigate the following problem:

$$\begin{cases} -\varepsilon\Delta_y u - u_{xx} - cu_x = \mu(M \star u - u) & \\ \qquad\qquad\qquad +u(a(y) - K \star u - \beta u) & \text{in } (-l,l) \times \Omega \\ \nabla_y u(x,y) \cdot \nu = 0 & \text{on } (-l,l) \times \partial\Omega \\ u(l,y) = 0 & \text{in } \Omega \\ u(-l,y) = p(y) & \text{in } \Omega, \end{cases} \tag{5.22}$$

for $\beta \geq 0$ and p solving (5.15). Notice that any solution to (5.15) is a subsolution to (5.14). In particular, we will use some solutions to (5.15) to get lower estimates on solutions to (5.14).

Let us also introduce the following quantity, which is the minimal speed for traveling waves (as we will show later):

$$c_\varepsilon^* := 2\sqrt{-\lambda_1^\varepsilon}. \tag{5.23}$$

Our result is the following:

Theorem 5.5.1 (Existence of solutions in the box)**.** *Let Assumption 5.2.2 hold, $\varepsilon > 0$ be such that $\lambda_1^\varepsilon < 0$, and $\beta \geq 0$. Then, there exists a nonnegative solution to* (5.22)*. Moreover, let $l_0 := \frac{\pi}{\sqrt{-\lambda_1^\varepsilon}} > 0$, $\nu_0 := \frac{-\lambda_1^\varepsilon}{2} > 0$. Then, for any $0 < \nu < \nu_0$, there exists $\bar{l}(\nu) \geq l_0 + 1$ such that if $l > \bar{l}(\nu)$, there exists a nonnegative solution (c,u) to* (5.22) *with $0 < c \leq c_\varepsilon^*$, which also satisfies the normalization condition*

$$\sup_{(x,y)\in(-l_0,l_0)\times\Omega} \left(\int_\Omega K(y,z)u(x,z)\mathrm{d}z + \beta u(x,y) \right) = \nu. \tag{5.24}$$

Before we prove Theorem 5.5.1, we need to establish some *a priori* estimates on the solutions to (5.22). For technical reasons, we actually study the solutions to

$$\begin{cases} -\varepsilon\Delta_y u - u_{xx} - cu_x = \sigma\big(\mu(M\star u - u) & \\ \qquad\qquad +u\chi_{u\geq 0}(a(y) - K\star u - \beta u)\big) & \text{in } (-l,l)\times\Omega \\ \nabla_y u(x,y)\cdot\nu = 0 & \text{on } \partial(-l,l)\times\Omega \\ u(l,y) = 0 & \text{in } \Omega \\ u(-l,y) = p(y) & \text{in } \Omega, \end{cases} \tag{5.25}$$

where $\chi_{u\geq 0} = \begin{cases} 0 \text{ if } u\leq 0 \\ 1 \text{ if } u>0 \end{cases}$, and $\sigma\in(0,1]$.

Lemma 5.5.2 (A priori estimates on the solutions to (5.25))**.** *Let Assumption 5.2.2 hold, $\varepsilon>0$ such that $\lambda_1^\varepsilon<0$, and $\beta\geq 0$. We define $l_0 := \frac{\pi}{\sqrt{-\lambda_1^\varepsilon}}$. Let u be a solution to (5.25), then*

(i) $u\in C^2_{loc}\big((-l,l)\times\Omega\big)\cap C^1_{loc}\big((-l,l)\times\overline{\Omega}\big)$.

(ii) *u is positive in $(-l,l)\times\overline{\Omega}$.*

(iii) *For any $x\in[-l,l]$, we have $\int_\Omega u(x,y)dy \leq \frac{\sup a}{k_0}$.*

(iv) *There exists C independent from c, l and σ such that $\|u\|_{C_b((-l,l)\times\Omega)}\leq C$. If $\beta>0$, then we have the estimate $\|u\|_{C_b((-l,l)\times\Omega)}\leq\frac{\sup a}{\beta}$.*

(v) *If $\sigma=1$, $c=0$, and $l>l_0$, then*

$$\sup_{(x,y)\in(-l_0,l_0)\times\Omega}\left(\int_\Omega K(y,z)u(x,z)\mathrm{d}z + \beta u(x,y)\right) > \frac{-\lambda_1^\varepsilon}{2}.$$

Remark that for this result to hold, u needs only to be defined on $(-l_0,l_0)\times\Omega$.

(vi) *If $\sigma=1$ and $c=c^*_\varepsilon$, then there exists a constant A (independent from l) and $\lambda:=\frac{c^*_\varepsilon}{2}>0$ such that*

$$\forall (x,y)\in(-l,l)\times\Omega, \qquad u\leq Ae^{-\lambda(x+l)}.$$

In particular for any $0<\nu\leq\nu_0=\frac{-\lambda_1^\varepsilon}{2}$ and $l\geq\bar{l}(\nu) := \frac{1}{\lambda}\ln\left(\frac{\nu}{2A(k_\infty\int_\Omega\varphi^\varepsilon+\beta\sup_\Omega\varphi^\varepsilon)}\right) - l_0$, we have

$$\sup_{(x,y)\in(-l_0,l_0)\times\Omega}\left(\int_\Omega K(y,z)u(x,z)\mathrm{d}z + \beta u(x,y)\right) < \nu.$$

Proof. We prove each point one by one.

Item (*i*): We first remark that if $u \in C^0$ is a weak solution to (5.25), then u is in fact a classical solution to (5.25). Indeed by a direct application of [27, Lemma 7.1], u is in $W^{2,p}_{loc}\big((-l,l)\times\Omega\big)\cap C([-l,l]\times\overline{\Omega})$ for any $p>0$ and thus, thanks to the Sobolev imbeddings [108, Theorem 7.26], in C^{α}_{loc}. It follows from the Schauder interior estimates [108, Corollary 6.3] that $u \in C^{2,\alpha}_{loc}$.

Moreover, using again [27, Lemma 7.1] and the Sobolev imbeddings, u is in fact $C^{1,\alpha}$ in a neighbourhood of any $y \in (-l,l)\times\partial\Omega$. In particular, the boundary condition $\frac{\partial u}{\partial \nu}(y)=0$ is satisfied in a classical sense for $y \in (-l,l)\times\partial\Omega$.

This proves item (i).

Item (*ii*): Assume u has a negative minimum at $(x_0,y_0)\in[-l,l]\times\Omega$. Then thanks to the boundary conditions satisfied by u, we have that $x_0 \in (-l,l)$. Assume $y \in \partial\Omega$, then near (x_0,y_0):

$$-u_{xx}-\varepsilon\Delta_y u - cu_x = \sigma\mu(M\star u-u)\geq 0,$$

thus Hopf's Lemma implies $\frac{\partial u}{\partial \nu}(y_0)<0$, which contradicts the Neumann boundary condition satisfied by u. Thus $y_0\in\Omega$. In particular

$$-u_{xx}(x_0,y_0)-\varepsilon\Delta_y u(x_0,y_0)-cu_x(x_0,y_0)=\sigma\mu(M\star u-u)(x_0,y_0)\geq 0$$

and the strong maximum principle leads to a contradiction. Thus $u\geq 0$. The positivity of u then follows by a direct application of the strong maximum principle and Hopf's Lemma.

This shows item (ii).

Item (*iii*): Thanks to Lemma 5.4.5, we have $\int_\Omega p(y)dy \leq \frac{\sup a}{k_0}$. Assume that $x\mapsto \int_\Omega u(x,y)dy$ has a maximal value at $x_0\in(-l,l)$, then integrating (5.25) over Ω we have

$$\begin{aligned}0 \leq -\frac{d^2\int_\Omega u(x_0,y)dy}{dx^2} - c\frac{d\int_\Omega u(x_0,y)dy}{dx}&\\ =\sigma\int_\Omega a(y)u(x_0,y)-(K\star u)(x_0,y)dy,&\end{aligned}$$

$$\begin{aligned}k_0\left(\int_\Omega u(x_0,y)dy\right)^2 &\leq \int_\Omega\int_\Omega K(y,z)u(x_0,z)u(x_0,y)dydz\\ &=\int_\Omega a(y)u(x_0,y)dy \leq \sup a\int_\Omega u(x_0,y)dy.\end{aligned}$$

This shows item (iii).

Item (*iv*): Assume first $\beta>0$ and let $(x,y)\in(-l,l)\times\Omega$ satisfy $u(x,y)=\sup u$. Assume by contradiction that $u(x,y)>\frac{\sup a}{\beta}$. If $x=-l$, then, since p satisfies $\sup p \leq \frac{\sup a}{\beta}$ thanks to 5.4.2 item (ii), we have a contradiction. If $x = +l$, since $u(x,y) = 0$, we have a contradiction. Assume $x \in (-l, l)$. If $y \in \partial\Omega$, then $\frac{\partial u}{\partial \nu}(x,y) > 0$ thanks to Hopf's Lemma, which contradicts the Neumann boundary conditions satisfied by u. Thus $y \in \Omega$. Now, testing (5.25) at (x,y), we have

$$\begin{aligned}0 &\leq -\varepsilon\Delta_y u(x,y) - u_{xx}(x,y) - cu_x(x,y) - \sigma\mu\big((M \star u)(x,y) - u(x,y)\big)\\ &= \sigma u(x,y)\big(a(y) - (K \star u)(x,y) - \beta u(x,y)\big) < 0\end{aligned}$$

which is a contradiction. Thus $u \leq \frac{\sup a}{\beta}$.

We turn our attention to the case $\beta = 0$. In this case, we construct a supersolution in a similar way we did in Lemma 5.4.2.

To obtain an interior bound for u, we look at the equation satisfied by $u(x,y) - p(y)$:

$$\begin{aligned}&-\varepsilon\Delta_y(u-p) - c(u-p)_x - (u-p)_{xx} - \sigma(a(y) - \mu - K \star u)(u-p)\\ &= \sigma\mu M \star u + (\sigma - 1)(a(y) - \mu)p + (K \star p)p - \sigma(K \star u)p - \mu M \star p\\ &\leq \sigma\mu M \star u + (\sigma - 1)(a(y) - \mu)p + (K \star p)p,\end{aligned}$$

where the right-hand side is bounded by a constant independent from l and σ. The local maximum principle up to the boundary [108, Theorem 9.26] shows the following property: for any ball $B_R(x,y) \subset (-l-R, l+R) \times \Omega$, we have

$$\begin{aligned}\sup_{B_{\frac{R}{2}}(x,y)} (u-p) \leq C\Bigg\{ &\frac{1}{|B_R(x,y)|}\int_{B_R(x,y)\cap(-l,l)\times\Omega} (u-p)^+ dxdy\\ &+ \frac{R}{\varepsilon}\|\mu M \star u + (\sigma-1)(a(y)-\mu)p + (K \star p)p\|_{L^n(B_R(x,y))}\Bigg\} \qquad (5.26)\end{aligned}$$

where $C = C(R, \varepsilon, \|a\|_{L^\infty}, k_0, k_\infty, \mu, c)$. This shows a uniform interior bound for u: there exists γ_R such that

$$u(x,y) \leq \gamma_R$$

for any y such that $d(y, \partial\Omega) \geq R$.

To show that this estimate does not degenerate near the boundary, we use the same kind of supersolution as in Lemma 5.4.2. Let

$$\Omega_R := \{y \in \Omega, d(y, \partial\Omega) \leq R\}$$

for any $R > 0$. As noted in [91], the function $y \mapsto d(y, \partial\Omega)$ is C^3 on a tubular neighbourhood of $\partial\Omega$. In particular, Ω_R has a C^3 boundary for $R > 0$ small enough. Moreover, by the comparison principle in narrow domains [27, Proposition 1.1], there exists $\delta > 0$ depending only on Ω,

$\|a\|_{L^\infty}$ and ε such that if $|\Omega_R| \leq \delta$, then the maximum principle holds for the operator $-\varepsilon\Delta v - \sigma(a(y) - \mu)v$ in Ω_R, meaning that if v satisfies $-\varepsilon\Delta v - \sigma(a(y) - \mu)v \geq 0$ in Ω_R and $v \geq 0$ on $\partial\Omega_R$, then $v \geq 0$. In particular, we choose R small enough for this property to holds. Let us stress that since $\sigma \in (0,1)$, R can be chosen uniformly in σ.

This allows us to construct a positive solution to

$$\begin{cases} -\varepsilon\Delta v - \sigma(a(y) - \mu)v = \mu m_0 \frac{m_\infty \sup a}{k_0} & \text{in } \Omega \\ v = \gamma_R & \text{on } \partial\Omega_R \backslash \partial\Omega \\ \frac{\partial v}{\partial \nu} = 0 & \text{on } \ \partial\Omega, \end{cases}$$

which is bounded uniformly in σ, as we did in the proof of Lemma 5.4.2. Now we select

$$\eta := \inf\{\zeta > 0, \forall x \in (-l,l), \forall y \in \Omega, \zeta v(y) \geq u(x,y)\}.$$

Assume by contradiction that $\eta > 1$. Then there exists $(x,y) \in [-l,l] \times \overline{\Omega}$ such that $u(x,y) = \eta v(y)$. If $x = l$ then $u = 0$, which is a contradiction. If $x = -l$, since $u(-l,y) = p(y)$ solves (5.14), we argue as in Lemma 5.4.2 and get a contradiction. We are left to investigate the case $x \in (-l,l)$. If $y \in \partial\Omega$, since (x,y) is a minimum to the function $\eta v - u$, then by Hopf's Lemma we have $\frac{\partial(\eta v - u)}{\partial \nu}(x,y) < 0$ which is a contradiction since both u and v satisfy a Neumann boundary value problem. Thus $y \notin \partial\Omega$. Since $\eta > 1$ and $u \leq \gamma_R$ for $y \in \partial\Omega_R\backslash\partial\Omega$, then $y \in \Omega_R$. Now (x,y) is a local minimum to $\eta v - u$ and thus

$$\begin{aligned} 0 \geq -\varepsilon\Delta(\eta v - u)(x,y) &= \sigma(a(y) - \mu)(\eta v - u)(x,y) + \eta\mu m_0 \frac{m_\infty \sup a}{k_0} \\ &\quad - \sigma\mu(M \star u)(x,y) + u(x,y)(K \star u)(x,y) \\ &> \eta\mu m_0 \frac{m_\infty \sup a}{k_0} - \sigma\mu(M \star u)(x,y) \geq 0 \end{aligned}$$

which is a contradiction. Thus $\eta \leq 1$.

This shows that $u \leq v$ in Ω_R. Since v is bounded uniformly in σ, we have our uniform bound for u in $[-l,l] \times \Omega_R$. In $(-l,l) \times \Omega\backslash\Omega_R$, thanks to (5.26), we have $u \leq \gamma_R$.

This proves item (iv).

Item (v): This proof is similar to the one in [5]. Assume by contradiction that

$$\sup_{(x,y)\in(-l_0,l_0)\times\Omega} \left(\int_\Omega K(y,z)u(x,z)\mathrm{d}z + \beta u(x,y) \right) \leq \nu_0.$$

Then u satisfies:

$$-u_{xx} - \varepsilon\Delta_y u - \mu(M \star u - u) - a(y)u \geq -\nu_0 u \tag{5.27}$$

in $(-l_0, l_0)$.

Define $\psi(x,y) := \cos\left(\frac{\pi}{2l_0}x\right)\varphi^\varepsilon(y)$, where φ^ε is the principal eigenfunction solution to (5.12) satisfying $\sup_{y\in\Omega}\varphi^\varepsilon = 1$. Since u is positive in $[-l_0, l_0]\times\overline{\Omega}$, we can define

$$\alpha := \sup\{\zeta > 0, \forall (x,y) \in (-l_0, l_0)\times\Omega, \quad \zeta\psi(x,y) \le u(x,y)\} > 0.$$

By definition of α there exists $(x,y) \in [-l_0, l_0]\times\overline{\Omega}$ such that $\alpha\psi(x,y) = u(x,y)$. If $x \in \{-l_0, l_0\}$ then $\psi(x,y) = 0$ and we have a contradiction. If $x \in (-l_0 l_0)$ and $y \in \partial\Omega$, since u and ψ both satisfy Neumann boundary conditions on $(-l_0, l_0)\times\partial\Omega$ and (x,y) is the minimum of $u - \alpha\psi$, we have a contradiction thanks to Hopf's Lemma. Thus $(x,y) \in (-l_0, l_0)\times\Omega$ and we have:

$$\begin{aligned}
0 &\ge -\varepsilon\Delta_y(u-\alpha\psi)(x,y) - (u-\alpha\psi)_{xx}(x,y) \\
&\quad - \mu\big(M \star (u-\alpha\psi) - (u-\alpha\psi)\big)(x,y) - a(y)(u-\alpha\psi)(x,y) \\
&\ge -\nu_0 u(x,y) + \alpha\left(-\lambda_1^\varepsilon - \left(\frac{\pi}{2l_0}\right)^2\right)\psi(x,y) \\
&= \left(\frac{-3\lambda_1^\varepsilon}{4} - \nu_0\right)u(x,y) > 0,
\end{aligned}$$

since $-\nu_0 = \frac{\lambda_1^\varepsilon}{2}$. This is a contradiction.

This proves item (v).

Item (*vi*): Let $\psi(x,y) := e^{-\frac{c_\varepsilon^*}{2}x}\varphi^\varepsilon(y)$ with. Then ψ satisfies:

$$\begin{aligned}
-c_\varepsilon^*\psi_x - \psi_{xx} - \varepsilon\Delta_y\psi - \mu(M\star\psi - \psi) &= \left(\frac{c_\varepsilon^*}{2}\left(c_\varepsilon^* - \frac{c_\varepsilon^*}{2}\right) + a(y) + \lambda_1^\varepsilon\right)\psi \\
&= \left(\frac{c_\varepsilon^{*2}}{4} + a(y) + \lambda_1^\varepsilon\right)\psi = a(y)\psi.
\end{aligned}$$

Since $\psi > 0$ on $[-l,l]\times\overline{\Omega}$, there exists $\zeta > 0$ such that $\zeta\psi \ge u$ on $(-l,l)\times\Omega$. Let us select

$$\alpha := \inf\{\zeta > 0, \forall (x,y) \in (-l_0, l_0)\times\Omega, \quad \zeta\psi(x,y) \ge u(x,y)\}.$$

By definition of α we have $\alpha\psi \ge u$ and there exists $(x,y) \in [-l,l]\times\overline{\Omega}$ such that $\alpha\psi(x,y) = u(x,y)$. If $x = l$ then $\psi(x,y) = 0$ and we have a contradiction. If $x \in (-l,l)$ and $y \in \partial\Omega$, since u and ψ both satisfy Neumann boundary conditions on $(-l,l)\times\partial\Omega$ and (x,y) is the zero maximum of $u-\alpha\psi$, we have a contradiction thanks to Hopf's Lemma. If $(x,y) \in (-l,l)\times\Omega$, we have:

$$\begin{aligned}
0 &\le -\varepsilon\Delta_y(u-\alpha\psi)(x,y) - (u-\alpha\psi)_{xx}(x,y) \\
&\quad - \mu\big(M \star (u-\alpha\psi) - (u-\alpha\psi)\big)(x,y) - a(y)(u-\alpha\psi)(x,y) \\
&= -(K\star u)(x,y)u(x,y) < 0
\end{aligned}$$

which is a contradiction. We conclude that $x = -l_0$ and thus

$$\alpha \leq \frac{\sup_\Omega p}{\inf_\Omega \varphi^\varepsilon} e^{-\frac{c_\varepsilon^*}{2} l}.$$

By definition of α, we can then write:

$$u(x,y) \leq \alpha e^{-\frac{c_\varepsilon^*}{2} x} \varphi^\varepsilon(y) \leq \frac{\sup_\Omega p}{\inf_\Omega \varphi^\varepsilon} e^{-\frac{c^*}{2}(x+l)} \varphi^\varepsilon(y)$$

which is the desired estimate.

This shows item (vi). □

We are now in the position to prove Theorem 5.5.1, thanks to the global continuation principle, stated in Appendix 5.6.3.

Proof of Theorem 5.5.1. For $c \in \mathbb{R}$ and $u \in C_b\big((-l,l) \times \Omega\big)$. We define $F(c,u) = \tilde{u}$ where $\tilde{u}$ solves:

$$\begin{cases} -\tilde{u}_{xx} - c\tilde{u}_x - \varepsilon \Delta_y \tilde{u} = \mu M \star u & \\ \qquad\qquad +u\chi_{u\geq 0}(a(y) - \mu - K \star u - \beta u) & \text{in } (-l,l) \times \Omega \\ \frac{\partial \tilde{u}}{\partial \nu}(x,y) = 0 & \text{on } (-l,l) \times \partial\Omega \\ \tilde{u}(l,y) = 0 & \text{in } \Omega \\ \tilde{u}(-l,y) = p(y). & \text{in } \Omega. \end{cases} \tag{5.28}$$

Thanks to [27, Lemma 7.1], $\tilde{u}$ is well-defined and belongs to $C_b([-l,l] \times \overline{\Omega}) \cap W^{2,p}_{loc}([-l,l] \times \overline{\Omega} \backslash \{-l,l\} \times \partial\Omega)$ for any $p > 0$.

Step 1: Let us briefly show that F is in fact a compact operator. Since the right-hand side of the first equation in (5.28) is bounded, it is easily seen that the function $(x,y) \mapsto \big(1 + \gamma(x+l)^\alpha\big)p(y)$ is a local supersolution to equation (5.28) near $x = l$ for $0 \leq \alpha < \alpha_0$, $\gamma \geq \gamma_0 > 0$, where α_0 and γ_0 depend only on $\|u\|_{C_b((-l,l)\times\Omega)}$, a bound for c and the data and coefficients of the problem. Similarily, $(1 - \gamma(x+l)^\alpha\big)p(y)$ is a local subsolution for α small enough. Thus $\big(1 - \gamma(x+l)^\alpha\big)p(y) \leq \tilde{u}(x,y) \leq \big(1 + \gamma(x+l)^\alpha\big)p(y)$ for $\alpha > 0$ small enough. In particular, the function $x \in [-l,0] \mapsto \tilde{u}(x,y)$ is uniformly in C^α for $y \in \overline{\Omega}$. It then follows from [108, Corollary 9.28] (and the classical interior Sobolev imbeddings) that $\tilde{u} \in C^\alpha([-l,0] \times \overline{\Omega})$. Regularity near $x = l$ is proven the same way. Thus $\tilde{u} \in C^\alpha([-l,l] \times \overline{\Omega})$ where α depends only on a bound for $\|u\|_{C_b((-l,l)\times\Omega)}$ and c, and the data and coefficients of problem (5.28). In particular, F maps bounded sets of $\mathbb{R} \times C_b((-l,l) \times \Omega)$ into relatively compact sets in $C_b((-l,l) \times \Omega)$.

Step 2: We aim at applying Theorem 5.6.5 to $F(0,\cdot)$. We remark that the solutions to $u = \sigma F(0,u)$ for $\sigma \in (0,1)$ are in fact the solutions to (5.25). In particular, Lemma 5.5.2 gives us a constant $C > 0$ such that any solution to (5.25) satisfies $\|u\|_{C_b(-l,l)\times\Omega} \leq C$. Let $G := \{u \in C_b((-l,l) \times \Omega), \|u\|_{C_b((-l,l)\times\Omega)} \leq 2C\}$, then

1. G is a bounded open subset of the Banach space $C_b((-l,l)\times\Omega)$,
2. $0\in G$,
3. $F(0,\cdot):G\to C_b((-l,l)\times\Omega)$ is a compact mapping, and
4. thanks to Lemma 5.5.2, there is no solution to $u=\sigma F(0,u)$ with $u\in\partial G$ and $\sigma\in(0,1]$.

Thus Theorem 5.6.5 applies and we have $ind(F(0,\cdot),G)=1$, where ind is the Leray-Schauder fixed-point index.

Step 3: Let us now check that the hypotheses of Theorem 5.6.6 are satisfied. We have:

1. F is a compact mapping from $(0,c_\varepsilon^*)\times\overline{G}$ into $C_b((-l,l)\times\Omega)$,
2. thanks to Lemma 5.5.2, there is no solution to $u=F(c,u)$ with $u\in\partial G$ and $c\in[0,c_\varepsilon^*]$, and
3. $ind(F(0,\cdot),G)=1$.

Thus, Theorem 5.6.6 applies and there exists a connected set of solutions $\mathcal{C}$ to $u=F(c,u)$ connecting $\{0\}\times G$ to $\{c_\varepsilon^*\}\times G$. In particular, there exists a solution to (5.22) for any $c\in[0,c_\varepsilon^*]$.

Step 4: Now let us assume $l\geq\bar{l}(\nu)$ (where $\bar{l}(\nu)$ is given by Lemma 5.5.2, item 5). Since the mapping

$$u\in C_b((-l,l)\times\Omega)\overset{N}{\longmapsto}\sup_{(x,y)\in(-l_0,l_0)\times\Omega}\int_\Omega K(y,z)u(x,z)dz+\beta u(x,y)$$

is continuous, then $N(\mathcal{C})$ is a connected subset of $\mathbb{R}$, i.e. an interval. Applying Lemma 5.5.2, we have:

– From point (v), if $(c,u)\in\mathcal{C}$ and $c=0$, then $N(u)>\nu$.

– From point (vi), if $(c,u)\in\mathcal{C}$ and $c=c_\varepsilon^*$ then $N(u)<\nu$.

Thus there exists $c\in(0,c_\varepsilon^*)$ and u such that $(c,u)\in\mathcal{C}$ and $N(u)=\nu$. This finishes the proof of Theorem 5.5.1. □

An immediate consequence is the following:

Corollary 5.5.3 (Existence of a solution on the line)**.** *Let Assumption 5.2.2 hold, $\varepsilon>0$ be such that $\lambda_1^\varepsilon<0$, $\beta\geq0$ and $0<\nu\leq\frac{-\lambda_1^\varepsilon}{2}$. Then there exists a classical positive solution to*

$$\begin{cases}-u_{xx}-cu_x=\varepsilon\Delta_y u+\mu(M\star u-u) & \\ \qquad\qquad +u(a(y)-K\star u-\beta u) & on\ \mathbb{R}\times\Omega \\ \frac{\partial u}{\partial\nu}=0 & on\ \mathbb{R}\times\partial\Omega,\end{cases}\tag{5.29}$$

with $0 < c \le c_*$*. Moreover* $u \in C_b(\mathbb{R}\times\Omega)\cap C^2(\mathbb{R}\times\overline{\Omega})$*, satisfies* (5.24) *and*

$$\forall x \in \mathbb{R}, \qquad \int_\Omega u(x,y)dy \le \frac{\sup a}{k_0}.$$

Proof. Let $0 < \nu \le \nu_0$ and $\bar{l} = \bar{l}(\nu)$ as in Theorem 5.5.1. Then thanks to Theorem 5.5.1, for any $n \in \mathbb{N}$, there exists a classical solution $(c_n, u_n) \in (0, c_\varepsilon^*)\times C^2((-l_n, l_n)\times\Omega)\cap C^1((-l_n,l_n)\times\overline{\Omega})$ to (5.22) which satisfies (5.24), where $l_n := \bar{l}+n$. Thanks to the uniform bound satisfied by $\sup u_n$ (Lemma 5.5.2 point (iv)), the classical Schauder interior estimates [108, Theorem 6.2] and the boundary Schauder estimates [108, Theorem 6.29], there exists a constant $C_k > 0$, independent from n such that

$$\|u_n\|_{C^{2,\alpha}((-l_k,l_k)\times\overline{\Omega})} \le C_k$$

for any $k < n$. Using a classical diagonal extraction process, we extract from (c_n, u_n) a subsequence such that $c_n \to c^0$, and $\|u_n - u\|_{C^2((-l_k,l_k)\times\overline{\Omega})} \to 0$ for any $k \in \mathbb{N}$. Then u solves (5.29), (5.24) and consequently thanks to Lemma 5.5.2 point (v), $c^0 > 0$. Moreover thanks to Lemma 5.5.2 point (iii), we have

$$\forall x \in \mathbb{R}, \qquad \int_\Omega u(x,y)dy \le \frac{\sup a}{k_0}.$$

This finishes the proof of Corollary 5.5.3. □

5.5.2 Proof of minimality for $\beta \ge \beta_0$

In the case $\beta \ge \beta_0 := \frac{k_\infty \sup a}{\mu m_0}$, we expect to recover a kind of comparison principle thanks to an algebraic trick. Roughly speaking, increasing competition (via large β) enforces the solution to remain in the region "u small" where the system is cooperative (see Lemma 5.5.5). We deduce then interesting properties on the solutions. In particular, we recover that the solution constructed in Corollary 5.5.3 satisfies $c = c_\varepsilon^*$ and is in fact a minimal speed traveling wave.

Theorem 5.5.4 (Minimal speed traveling waves for $\beta \ge \beta_0$)**.** *Let Assumption 5.2.2 hold,* $0 < \varepsilon \le \varepsilon_0$ *— where* ε_0 *is as in Lemma 5.4.4— be such that* $\lambda_1^\varepsilon < 0$*, and* $\beta \ge \beta_0 = \frac{k_\infty \sup a}{\mu m_0}$*. Then, there exists a solution* (c, u) *to* (5.29) *satisfying* $c = c_\varepsilon^*$ *and the limit conditions*

$$\liminf_{x\to-\infty}\inf_{y\in\Omega} u(x,y) > 0, \qquad \lim_{x\to+\infty}\sup_{y\in\Omega} u(x,y) = 0. \tag{5.30}$$

Moreover, u *is nonincreasing in* x*, and there exists no positive solution to* (5.29) *satisfying* (5.30) *and* $0 \le c < c_\varepsilon^*$*.*

Finally, we have

$$\lim_{x\to-\infty}\inf_{y\in\Omega} u(x,y) \ge \rho_\beta$$

where ρ_β *is the constant defined in Lemma 5.4.4.*

Our main tool is the following *comparison principle* for small densities.

Lemma 5.5.5 (Comparison principle for small densities)**.** *Let Assumption 5.2.2 hold and $\beta \geq 0$. Let $u \in C^2$ be a supersolution to*

$$-cu_x - u_{xx} - \varepsilon\Delta_y u - \mu(M \star u - u) - u(a(y) - K \star u - \beta u) \geq 0 \quad (5.31)$$

and $v \in C^2$ be a subsolution to

$$-cv_x - v_{xx} - \varepsilon\Delta_y v - \mu(M \star v - v) - v(a(y) - K \star v - \beta v) \leq 0. \quad (5.32)$$

If there exists $(x_0, y_0) \in \mathbb{R} \times \Omega$ such that $0 < u(x_0, y_0) \leq \frac{\mu m_0}{k_\infty}$, $u \geq v$ in a neighbourhood of $\{x_0\} \times \Omega$, and $u(x_0, y_0) = v(x_0, y_0)$, then $u \equiv v$.

Proof. Let (x_0, y_0) as in Lemma 5.5.5. Then (x_0, y_0) is a local zero minimum to $u - v$. We have:

$$-c(u-v)_x(x_0, y_0) - (u-v)_{xx}(x_0, y_0) - \varepsilon\Delta_y(u-v)(x_0, y_0) \leq 0$$

and thus:

$$\mu\big(M\star(u-v)-(u-v)\big)+a(y)(u-v)-uK\star u+vK\star v-\beta u^2+\beta v^2 \leq 0. \quad (5.33)$$

Using the fact that $u(x_0, y_0) = v(x_0, y_0)$, we rewrite (5.33) as

$$\int_\Omega \big(\mu M(y_0, z) - u(x_0, y_0)K(y_0, z)\big)\Big(\big(u(x_0, z) - v(x_0, z)\big) - \big(u(x_0, y_0) - v(x_0, y_0)\big)\Big)dz \leq 0.$$

Since $\mu M(y_0, z) - u(x_0, y_0)K(y_0, z) > 0$ for any $z \in \Omega$ and $u(x_0, y) - v(x_0, y) \geq 0$ for any $y \in \Omega$, we conclude that

$$\forall y \in \Omega, u(x_0, y) = v(x_0, y).$$

We get the desired conclusion by applying the strong maximum principle to $(u - v)$. This ends the proof of Lemma 5.5.5. □

Lemma 5.5.6 (Estimates for $\beta \geq \frac{k_\infty \sup a}{\mu m_0}$)**.** *Assume $\beta \geq \beta_0 = \frac{k_\infty \sup a}{\mu m_0}$. Then there exists a unique solution to* (5.22)*. Moreover, the solution to* (5.22) *is decreasing in x, and the mapping $c \mapsto u$ is decreasing.*

Proof. We divide the proof in four steps. Recall that, thanks to Theorem 5.5.1, there exists a solution to (5.22).

Step 1: We first show that any solution satisfies $u(x, y) < p(y)$ at any interior point. Let us define:

$$\alpha := \sup\{\zeta > 0, \zeta u \leq p\}.$$

Since u is bounded and p is positive on $\overline{\Omega}$, α is well-defined and positive. Assume by contradiction that $\alpha < 1$. By definition of α, there exists $(x, y) \in [-l, l] \times \overline{\Omega}$ such that $p(y) = \alpha u(x, y)$. Since $\alpha u(-l, y) = \alpha p(y) < p(y)$ and $\alpha u(l, y) = 0 < p(y)$, we have $x \in (-l, l)$. If $y \in \partial\Omega$, then thanks to Hopf's Lemma we have $\frac{\partial p - \alpha u}{\partial \nu}(x, y) < 0$, which contradicts the Neumann boundary conditions satisfied by u and p. Thus $y \in \Omega$. Next we remark that

$$\begin{aligned} &- c(\alpha u)_x - (\alpha u)_{xx} - \varepsilon\Delta_y(\alpha u) - \mu\big(M \star (\alpha u) - (\alpha u)\big) - a(y)(\alpha u) \\ &\qquad = (\alpha u)(-K \star u - \beta u) < \alpha u\big(- K \star (\alpha u) - \beta(\alpha u)\big), \end{aligned}$$

since $\alpha < 1$. Hence αu is a subsolution to (5.32). Moreover p is a supersolution to (5.31). Finally, thanks to Lemma 5.5.2 point (*iv*) and the condition $\beta \geq \beta_0$, we have $\|u\|_{L^\infty} \leq \frac{\sup a}{\beta} \leq \frac{\mu m_0}{k_\infty}$, and by definition (x, y) is the global minimum of $(p - \alpha u)$. Thus Lemma 5.5.5 applies and $\alpha u = p$, which is a contradiction.

Thus $\alpha \geq 1$, which shows that $u \leq p$. Assume now $u(x, y) = p(y)$ for some $(x, y) \in (-l, l) \times \Omega$, then Lemma 5.5.5 applies and we have $u = p$ in $(-l, l) \times \Omega$, which is again a contradiction. We conclude that the strict inequality holds:

$$\forall (x, y) \in (-l, l) \times \Omega, \qquad u(x, y) < p(y).$$

Step 2: We show that the solution u is unique. Here we use a sliding argument. Let u, v be two solutions to (5.22), and define:

$$\bar{x} := \inf\{\gamma > 0, \forall (x, y) \in (-l, l) \times \Omega, u(x + \gamma, y) \leq v(x, y)\}.$$

Thanks to the Dirichlet boundary conditions satisfied by u and v, we have that $0 \leq \bar{x} < 2l$. Assume by contradiction that $\bar{x} > 0$. We remark that $(x, y) \mapsto u(x + \bar{x}, y)$ is a subsolution to (5.32). By definition of $\bar{x}$, there exists $(x, y) \in (-l, l - \bar{x}) \times \Omega$ such that $u(x + \bar{x}, y) = v(x, y)$. In view Lemma 5.5.5, this leads to a contradiction. Thus $\bar{x} \leq 0$ and $u \leq v$. Exchanging the roles of u and v, we have in turn $v \leq u$. This shows the uniqueness of u.

Step 3: We show that $x \mapsto u(x, y)$ is decreasing. Repeating the argument in Step 2 with $u = v$, we have

$$\forall \bar{x} > 0, \forall (x, y) \in (-l, l) \times \Omega, \quad u(x + \bar{x}, y) \leq u(x, y).$$

which shows that u is nonincreasing. Moreover, equality cannot hold at an interior point in the above inequality, for Lemma 5.5.5 would lead to a contradiction. This shows that $x \mapsto u(x, \cdot)$ is decreasing.

Step 4: We show that $c \mapsto u$ is decreasing. Let $\bar{c} \leq c$, u (resp. v) be the solution to (5.22) associated with the speed c (resp. $\bar{c}$). Let also:

$$\bar{x} := \inf\{\gamma > 0, \forall y \in \Omega, u(x + \gamma, y) \leq v(x, y)\}$$

and assume by contradiction that $\bar{x} > 0$. Then

$$\begin{aligned}-cv_x - v_{xx} - \varepsilon\Delta_y v &= \mu(M \star v - v) + v(a - K \star u - \beta u) + (\bar{c} - c)v_x \\ &\geq \mu(M \star v - v) + v(a - K \star u - \beta u),\end{aligned}$$

since, as shown above, $v_x \leq 0$. Thus v is a supersolution to (5.31) and Lemma 5.5.5 then leads to a contradiction. Thus $c \mapsto u$ is nonincreasing. Moreover if $\bar{c} < c$, then we deduce from the above argument that $v > u$. Hence $c \mapsto u$ is in fact decreasing.

This ends the proof of Lemma 5.5.6. □

In particular, we notice that:

Corollary 5.5.7 (Existence of monotone fronts for β large)**.** *Let $\beta \geq \beta_0 = \frac{k_\infty \sup a}{\mu m_0}$. Then the solution constructed in Corollary 5.5.3 is decreasing in x.*

The next results shows that if u is a traveling wave, then $c \geq c_\varepsilon^*$.

Lemma 5.5.8 (c_ε^* is the minimal speed)**.** *Let Assumption 5.2.2 hold, $\varepsilon > 0$ be such that $\lambda_1^\varepsilon < 0$, and u be a positive solution to* (5.29) *with $0 \leq c \leq c_\varepsilon^*$ and either*

(i) $\beta > 0$ *and* $\lim_{x\to+\infty} \sup_{y\in\Omega} u(x,y) = 0$*, or*

(ii) $\beta = 0$ *and* $\lim_{x\to+\infty} \int_\Omega u(x,y)dy = 0$.

Then $c = c_\varepsilon^*$.

Proof. It follows from our hypothesis (i) or (ii) that we can find arbitrary large intervals $[\bar{x} - L, \bar{x} + L]$ on which

$$\sup_{(x,y)\in(\bar{x}-L,\bar{x}+L)\times\Omega} \left(\int_\Omega K(y,z)u(x,z)dz + \beta u(x,y) \right) \leq \delta, \tag{5.34}$$

for arbitrarily small $\delta > 0$. Since equation (5.29) is invariant by translation in x, we may assume w.l.o.g. that $\bar{x} = 0$.

Assume by contradiction that $c < c_\varepsilon^*$ and define

$$\theta := \sqrt{\frac{(c_\varepsilon^*)^2 - c^2}{8}},\ L := \frac{\pi}{2\theta},\ \delta := \frac{-\lambda_1^\varepsilon}{4} > 0,$$

and $\psi(x,y) := e^{-\frac{c}{2}x}\cos(\theta x)\varphi^\varepsilon(y)$, where φ^ε is the principal eigenfunction solution to (5.12) satisfying $\sup_{y\in\Omega}\varphi^\varepsilon = 1$. ψ satisfies

$$-c\psi_x - \psi_{xx} - \varepsilon\Delta_y\psi - \mu(M \star \psi - \psi) = a(y)\psi + \left(\frac{c^2}{4} + \theta^2 + \lambda_1^\varepsilon\right)\psi.$$

Since u is positive in $[-L, L] \times \overline{\Omega}$, we can define

$$\alpha := \sup\{\zeta > 0, \forall (x, y) \in (-L, L) \times \Omega, \quad \zeta\psi(x, y) \leq u(x, y)\} > 0.$$

By definition of α there exists $(x, y) \in [-L, L] \times \overline{\Omega}$ such that $\alpha\psi(x, y) = u(x, y)$. If $x \in \{-L, L\}$ then $\psi(x, y) = 0$ and we have a contradiction. If $x \in (-L, L)$ and $y \in \partial\Omega$, since u and ψ both satisfy Neumann boundary conditions on $(-L, L) \times \partial\Omega$ and (x, y) is the minimum of $u - \alpha\psi$, we have a contradiction thanks to Hopf's Lemma. Thus $(x, y) \in (-L, L) \times \Omega$ and, since u satisfies (5.34) we have

$$\begin{aligned}
0 &\geq -\varepsilon\Delta_y(u - \alpha\psi)(x, y) - (u - \alpha\psi)_{xx}(x, y) \\
&\quad - \mu\big(M \star (u - \alpha\psi) - (u - \alpha\psi)\big)(x, y) - a(y)(u - \alpha\psi)(x, y) \\
&\geq -\delta u(x, y) - \alpha\left(\frac{c^2}{4} + \theta^2 + \lambda_1^\varepsilon\right)\psi(x, y) \\
&= \left(-\delta - \frac{c^2}{8} - \frac{3\lambda_1^\varepsilon}{4}\right)u(x, y) \geq \left(-\delta - \frac{\lambda_1^\varepsilon}{2}\right) > 0,
\end{aligned}$$

since $\delta = \frac{-\lambda_1^\varepsilon}{4}$. This is a contradiction. □

Lemma 5.5.9 (Estimate on positive infima)**.** *Let Assumption 5.2.2 hold, $0 < \varepsilon \leq \varepsilon_0$ and $\beta \geq 0$, where ε_0 is as in Lemma 5.4.4. Assume $\lambda_1^\varepsilon < 0$. Let u be a solution to* (5.29) *which satisfies* $\inf_{(x,y)\in\mathbb{R}\times\Omega} u(x, y) > 0$*. Then*

$$\inf_{(x,y)\in\mathbb{R}\times\Omega} u(x, y) \geq \rho_{\max(\beta,\beta_0)}$$

where ρ_β is the constant from Lemma 5.4.4.

Proof. For any $\beta' \geq 0$, let $p^{\beta'}$ be a nonnegative nontrivial solution to (5.15). Since $\inf u > 0$ and $\sup p^{\beta'} \leq \frac{\sup a}{\beta'}$ (thanks to Lemma 5.4.2 item (*ii*)), there exists a constant $\beta' > 0$ such that

$$\beta' = \inf\{B > 0, p^B \leq u\}.$$

Assume by contradiction that $\beta' > \max(\beta, \beta_0)$. Then two cases may occur:

1. Assume there exists $(x_0, y_0) \in \mathbb{R} \times \overline{\Omega}$ such that

$$u(x_0, y_0) = p^{\beta'}(y_0).$$

Assume by contradiction that $y_0 \in \partial\Omega$. Then y_0 is the minimum of $u - p^{\beta'}$ and thanks to Hopf's Lemma, we have $\frac{\partial(u-p^{\beta'})}{\partial\nu}(x_0, y_0) < 0$, which contradicts the Neumann boundary conditions satisfied by u and $p^{\beta'}$. Thus $y_0 \in \Omega$.

Then, $p^{\beta'}$ is a subsolution to (5.29) (with $\beta = \beta$), $u \geq p^{\beta'}$ and since $\beta' > \beta_0$ we have $\|p^{\beta'}\|_{C_b(\Omega)} < \frac{\mu m_0}{k_\infty}$. Thus Lemma 5.5.5 applies and $u = p^{\beta'}$. Since $\beta' \neq \beta$, this is a contradiction.

2. If the latter does not hold, then by definition of β' there exists a sequence (x_n, y_n) such that $u(x_n, y_n) - p^{\beta'}(y_n) \to 0$. Since Ω is bounded, up to an extraction we have $y_n \to y_0 \in \overline{\Omega}$. Then

$$u(x_n, y_n) \to_{n\to\infty} p^{\beta'}(y_0).$$

Since equation (5.29) is invariant by translation in x, we consider the sequence $u^n(x, y) := u(x+x^n, y)$ which also satisfies (5.29). Then from the standard elliptic estimates and up to an extraction, u^n converges locally uniformly to u^∞, which is a classical solution to (5.29) and also satisfies

$$u^\infty(0, y_0) = p^{\beta'}(y_0), \qquad \forall x, y, u^\infty(x, y) \geq p^{\beta'}(y).$$

Item 1 then leads to a contradiction.

We have shown that either case leads to a contradiction if $\beta' > \max(\beta, \beta_0)$. Hence $\beta' \leq \max(\beta, \beta_0)$ and we conclude thanks to Lemma 5.4.4 that $u \geq \rho_{\max(\beta,\beta_0)}$. □

Proof of Theorem 5.5.4. Let $\nu := \frac{1}{2}(k_0|\Omega| + \beta)\rho_\beta$, where ρ_β is the constant from Lemma 5.4.4, and u be the correponding solution to (5.29), i.e. a solution to (5.29) constructed in Corollary 5.5.3, which satisfies

$$\sup_{(x,y)\in(-l_0,l_0)\times\Omega} \left(\int_\Omega K(y, z)u(x, z)dz + \beta u(x, y) \right) = \nu = \frac{1}{2}(k_0|\Omega| + \beta)\rho_\beta. \tag{5.35}$$

Recall that, thanks to Corollary 5.5.7, $x \mapsto u(x, y)$ is decreasing.

We divide the proof in three steps.

Step 1: We show that $\inf_{(x,y)\in\mathbb{R}\times\Omega} u(x, y) = 0$.

Indeed, thanks to (5.35), we have

$$\begin{aligned}(k_0|\Omega| + \beta)u(0, 0) &\leq \sup_{(x,y)\in(-l_0,l_0)\times\Omega} \int_\Omega K(y, z)u(x, z)dz + \beta u(x, y) \\ &= \frac{1}{2}(k_0|\Omega| + \beta)\rho_\beta,\end{aligned}$$

and thus $u(0, 0) \leq \frac{1}{2}\rho_\beta < \rho_\beta$. The contrapositive of Lemma 5.5.9 concludes.

Step 2: We show that $\lim_{x\to+\infty} \sup_{y\in\Omega} u(x, y) = 0$.

Thanks to Step 1, we have $\inf u = 0$. Since $u(x, y) > 0$ for $(x, y) \in \mathbb{R} \times \overline{\Omega}$ and u is decreasing in x, we must then have $\lim_{x\to+\infty} \inf_{y\in\Omega} u(x, y) = 0$.

Let $u^n(x, y) := u(x - n, y)$ and y_n such that $u^n(0, y_n) = \inf_{y\in\Omega} u^n(0, y)$. Since Ω is bounded, up to an extraction there exists $y \in \overline{\Omega}$ such that $y_n \to y_0$. Thanks to the classical elliptic estimates, we then extract from (u^n) a subsequence that converges locally uniformly on $\mathbb{R} \times \Omega$ to a limit function u^0, which is still a classical solution to (5.29).

Since u is decreasing, we have $\lim_{x\to+\infty}\sup_{y\in\Omega} u(x,y)=\sup_{y\in\Omega} u^0(0,y)$, and $0=\lim_{x\to+\infty}\inf_{y\in\Omega} u(x,y)=\inf_{y\in\Omega} u^0(0,y)=u(0,y_0)$. If $y_0\in\partial\Omega$ and $u^0\not\equiv 0$, then thanks to Hopf's Lemma we have $\frac{\partial u^0}{\partial\nu}(y_0)<0$, which contradicts the Neumann boundary conditions satisfied by u^0. If $y\in\Omega$ and the strong maximum principle imposes $u^0\equiv 0$. In either case, we have $u^0\equiv 0$ and thus $\lim_{x\to+\infty}\sup_{y\in\Omega} u(x,y)=0$.

Step 3: We show that $\lim_{x\to-\infty}\inf_{y\in\Omega} u(x,y)\geq\rho_\beta$.

Let $u^n(x,y):=u(x+n,y)$. Thanks to the classical elliptic estimates, we then extract from (u^n) a subsequence that converges locally uniformly on $\mathbb{R}\times\Omega$ to a limit function u^0, which is still a classical solution to (5.29).

Since u is decreasing, for any $\bar{x}\in\mathbb{R}$ we have $\lim_{x\to-\infty}\inf_{y\in\Omega} u(x,y)=\inf_{y\in\Omega} u^0(\bar{x},y)$ In particular, $\inf_{(x,y)\in\mathbb{R}\times\Omega} u^0(x,y)>0$. Applying Lemma 5.5.9, we conclude that $\lim_{x\to-\infty}\inf_{y\in\Omega} u(x,y)=\inf_{(x,y)\in\mathbb{R}\times\Omega} u^0(x,y)\geq\rho_\beta$.

To conclude the proof of Theorem 5.5.4, we remark that Lemma 5.5.8 states that $0\leq c<c_\varepsilon^*$ is incompatible with $\lim_{x\to+\infty}\sup_{y\in\Omega} u(x,y)=0$ with $0\leq c<c_\varepsilon^*$. This shows that $c=c_\varepsilon^*$. This finishes the proof of Theorem 5.5.4. □

5.5.3 Construction of a minimal speed traveling wave for $\beta=0$

Here we construct traveling waves for our initial regularized problem

$$\begin{cases} -\varepsilon\Delta_y u-u_{xx}-cu_x=\mu(M\star u-u)+u(a(y)-K\star u) & \text{in } \mathbb{R}\times\Omega \\ \frac{\partial u}{\partial\nu}=0 & \text{on } \mathbb{R}\times\partial\Omega. \end{cases} \tag{5.36}$$

Notice that (5.36) is exactly the equation (5.29) in the special case $\beta=0$. In particular, our results obtained in Corollary 5.5.3 and Lemmas 5.5.5, 5.5.8 and 5.5.9 still apply to the solutions of (5.36).

Our result is the following:

Theorem 5.5.10 (On regularized minimal speed traveling waves)**.** *Let Assumption 5.2.2 hold,* $0<\varepsilon\leq\varepsilon_0$ *(where* ε_0 *is as in Lemma 5.4.4) and assume* $\lambda_1^\varepsilon<0$. *Then, there exists a nonnegative nontrivial traveling wave* (c,u) *for* (5.36) *with* $c=c_\varepsilon^*$, *i.e. a bounded classical solution which satisfies:*

$$\liminf_{x\to-\infty}\inf_{y\in\Omega} u(x,y)>0,\qquad \limsup_{x\to+\infty}\int_\Omega u(x,y)dy=0. \tag{5.37}$$

Moreover, c_ε^* *is the minimal speed for traveling waves in the sense that there is no traveling wave for equation* (5.36) *with* $0<c\leq c_\varepsilon^*$.

Finally, u *can be chosen so that* $\sup_{x\in\mathbb{R}}\int_\Omega u(x,y)dy\leq\frac{\sup a}{k_0}$ *and*

$$\liminf_{x\to-\infty}\inf_{y\in\Omega} u(x,y)\geq\rho_{\beta_0},$$

where $\beta_0=\frac{k_\infty\sup a}{\mu m_0}$ *and* ρ_{β_0} *is given by Lemma 5.4.4.*

A key element for the proof of Theorem 5.5.10 is the following Harnack-type inequality, which allows us to show that $\inf_{y\in\Omega} u(x,y)$ and $\int_\Omega u(x,y)dy$ are locally comparable.

Lemma 5.5.11 (Harnack inequality for the mass)**.** *Let Assumption 5.2.2 hold and $\varepsilon > 0$. Let $\bar{c} > 0$, $R > 0$ and $W > 0$ be given. Let (c, u) be a solution to* (5.36) *with $|c| \leq \bar{c}$, $u \geq 0$ and $\int_\Omega u(x,y)dy \leq W$ for $x \in (-R, R)$. Then, there exists a constant $\mathcal{H} > 0$ depending only on R, $\|a\|_{L^\infty}$, W, k_∞ and $\bar{c}$ such that*

$$\sup_{|x|\leq R} \int_\Omega u(x,z)dz \leq \mathcal{H} \inf_{|x|\leq R} \int_\Omega u(x,z)dz.$$

Proof. Let $I(x) := \int_\Omega u(x,y)dy$, then I solves

$$\begin{aligned} -cI_x - I_{xx} &= \int_\Omega a(y)u(x,y)dy - \int_\Omega (K\star u)(y)u(x,y)dy \\ &= \left(\int_\Omega a(y)\frac{u(x,y)}{\int_\Omega u(x,z)dz}dy - \int_\Omega K\star u(x,y)\frac{u(x,y)}{\int_\Omega u(x,z)dz}dy\right) I. \end{aligned}$$

Now we remark that:

$$\left|\int_\Omega a(y)\frac{u(x,y)}{\int_\Omega u(x,z)dz}dy\right| \leq \|a\|_{L^\infty},$$

$$0 \leq \int_\Omega K\star u(x,y)\frac{u(x,y)}{\int_\Omega u(x,z)dz}dy \leq \|K\star u\|_{L^\infty} \leq k_\infty \int_\Omega u(x,y)dy \leq k_\infty W,$$

for any $x \in \mathbb{R}$, so that the classical Harnack inequality [108, Corollary 9.25] applies. □

Lemma 5.5.12 (Comparison between $\inf_y u(x,y)$ and $\int u(x,y)dy$)**.** *Let Assumption 5.2.2 hold and $\varepsilon > 0$. Let $\bar{c} > 0$, $x_0 \in \mathbb{R}$, $\kappa > 0$ and $W > 0$ be given. Let (c, u) be a solution to* (5.36) *with $|c| \leq \bar{c}$, $u \geq 0$ and $\int_\Omega u(x,y)dy \leq W$ for $|x - x_0| \leq 1$. Assume*

$$\int_\Omega u(x_0,y)dy \geq \kappa.$$

Then, there exists a positive constant $\bar{\kappa}$ depending only on $\|a\|_{L^\infty}$, μ, m_0, k_∞, $\bar{c}$, W and κ such that

$$\inf_{y\in\Omega} u(x_0,y) \geq \bar{\kappa}.$$

Proof. Since (5.36) is translation-invariant in x, we will assume w.l.o.g. that $x_0 = 0$.

Step 1: We construct a local subsolution.

From Lemma 5.5.11 there exists a constant $\mathcal{H} > 0$ such that

$$\kappa \leq \sup_{x\in(-1,1)} \int_\Omega u(x,z)dz \leq \mathcal{H} \inf_{x\in(-1,1)} \int_\Omega u(x,z)dz \leq \mathcal{H}\kappa.$$

Thus u satisfies:

$$-cu_x - u_{xx} - \varepsilon\Delta_y u \geq \mu m_0 \frac{\kappa}{\mathcal{H}} + \left(\inf_\Omega a - \mu - k_\infty W\right) u.$$

In particular there exists constants $\gamma > 0$ and $\alpha > 0$ depending only on $\|a\|_{L^\infty}$, μ , m_0, k_∞, W and κ such that

$$-cu_x - u_{xx} - \varepsilon\Delta_y u \geq \gamma - \alpha u \tag{5.38}$$

We define, for $\theta := \frac{2}{\sqrt{c^2+4\alpha}} \operatorname{asinh}\left(\frac{c}{2\sqrt{\alpha}}\right)$,

$$f^\delta(x) := \frac{\gamma}{\alpha} - \delta e^{-\frac{c}{2}(x-\theta)} \cosh\left(\frac{x-\theta}{2}\sqrt{c^2+4\alpha}\right).$$

Then f^δ satisfes

$$-cf^\delta_x - f^\delta_{xx} = \gamma - \alpha f^\delta.$$

In particular, f^δ satisfies equality in (5.38). Moreover for any $\delta > 0$, f^δ has a unique maximum located at 0 and $f^\delta \to -\infty$ as $x \to \pm\infty$. Finally, the mapping $\delta \mapsto f^\delta$ is decreasing.

Step 2: We identify δ_0 such that $u \geq f^{\delta_0}$.

Let $\delta_0 := \inf\{\delta > 0, \forall x \in (-1,1), f^\delta \leq u\}$. We claim that either $f^{\delta_0}(1) \geq 0$ or $f^{\delta_0}(-1) \geq 0$. Indeed, assume that contradiction that $f^{\delta_0}(-1) < 0$ and $f^{\delta_0}(1) < 0$. Then there exists $x_0 \in (-1,1)$, $y_0 \in \overline{\Omega}$ such that $u(x_0,y_0) = f^{\delta_0}(x_0)$. If $y_0 \in \partial\Omega$, then thanks to Hopf's Lemma we have $\frac{\partial(u-f^{\delta_0})}{\partial\nu}(x_0,y_0)$ since 0 is a minimum for the function $u-f^{\delta_0}$. This contradicts the Neumann boundary condition satisfied by u since $\frac{\partial f^{\delta_0}}{\partial\nu}(x_0,y_0) = 0$. If $y_0 \in \Omega$, we have

$$\begin{aligned} &- c(u-f^{\delta_0})_x(x_0,y_0) - (u-f^{\delta_0})_{xx}(x_0,y_0) - \varepsilon\Delta_y(u-f^{\delta_0})(x_0,y_0) \\ &\qquad\qquad \geq \big(\gamma - \alpha u(x_0,y_0)\big) - \big(\gamma - \alpha f^{\delta_0}(x_0,y_0)\big) = 0. \end{aligned}$$

Thanks to the strong maximum principle, we have then $u = f^{\delta_0}$ in $(-1,1)\times\overline{\Omega}$, which is a contradiction since f^{δ_0} is not positive in $(-1,1)$.

Step 3: We show that δ_0 is bounded by a constant depending only on $\bar{c}$, α and γ.

Let $\delta_1^c := \inf\{\delta > 0, f^\delta(-1) < 0 \text{ and } f^\delta(1) < 0\}$. δ_1^c is well-defined since $\lim_{\delta\to+\infty} f^\delta(\pm1) = -\infty$ and $\lim_{\delta\to0} f^\delta(\pm1) = \frac{\gamma}{\alpha} > 0$. Moreover, we have either $f^{\delta_1^c}(1) = 0$ or $f^{\delta_1^c}(-1) = 0$. Thus

$$\delta_1^c = \frac{\gamma}{\alpha} \max\left(\frac{e^{\frac{c}{2}(1-\theta)}}{\cosh\left(\frac{1-\theta}{2}\sqrt{c^2+2\alpha}\right)}, \frac{e^{\frac{c}{2}(-1-\theta)}}{\cosh\left(\frac{-1-\theta}{2}\sqrt{c^2+2\alpha}\right)}\right).$$

Since $\theta = \frac{2}{\sqrt{c^2+4\alpha}}\text{asinh}\left(\frac{c}{2\sqrt{\alpha}}\right)$ depends continuously on c, the mapping $c \mapsto f^{\delta_1^c}(0)$ is continuous. Moreover for any $|c| \leq \bar{c}$, $f^{\delta_1^c}(0) > 0$ since $x = 0$ is the strict maximum of $f^{\delta_1^c}$. Finally $\delta_0 \leq \delta_1^c$ since the mapping $\delta \mapsto f^\delta$ is decreasing. We have then

$$\inf_{y\in\Omega} u(0,y) \geq \inf_{|c|\leq\bar{c}} f^{\delta_1^c}(0) > 0$$

where the right-hand side depends only on $\bar{c}$, α and γ. This finishes the proof of Lemma 5.5.12. $\square$

Lemma 5.5.13 (Infimum estimate on the left)**.** *Let Assumption 5.2.2 hold, $0 < \varepsilon \leq \varepsilon_0$ be such that $\lambda_1^\varepsilon < 0$ (where ε_0 is given by Lemma 5.4.4), $\beta \geq \beta_0 = \frac{k_\infty \sup a}{\mu m_0}$ and u be a solution to* (5.36) *with $0 \leq c \leq c_\varepsilon^*$. Suppose*

$$\forall y \in \Omega, \quad u(0,y) \geq 2\frac{\sup a}{\beta}.$$

Then,

$$\forall x \leq 0, y \in \Omega, \quad u(x,y) \geq \rho_\beta$$

where ρ_β is given by Lemma 5.4.4.

Proof. We divide the proof in two step.

Step 1: We show that $\inf_{x\leq 0, y\in\Omega} u(x,y) > 0$.

Let φ^ε be the solution to (5.12). We normalize φ^ε so that

$$\sup_{y\in\Omega} \varphi^\varepsilon(y) = \frac{1}{2}\min\left(\inf_{y\in\Omega} u(0,y), \frac{-\lambda_1^\varepsilon}{|\Omega|k_\infty}, \frac{\mu m_0}{k_\infty}\right) > 0.$$

We define now:

$$\alpha := \sup\{\zeta > 0, \forall x \in (-\infty,0), y \in \Omega, (1+\zeta x)\varphi^\varepsilon(y) \leq u(x,y)\}.$$

Remark that, since u is positive and $\varphi^\varepsilon(y) < u(0,y)$ for any $y \in \mathbb{R}$, α is well-defined.

Assume by contradiction that $\alpha > 0$. Then by definition of α there exists $(x_0,y_0) \in \left(-\frac{1}{\alpha}, 0\right) \times \overline{\Omega}$ such that $u(x_0,y_0) = (1+\alpha x_0)\varphi^\varepsilon(y_0)$. Assume

$y_0 \in \partial\Omega$, then we have for (x, y) in a neighbourhood of (x_0, y_0),

$$
\begin{aligned}
&- c\big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big)_x - \big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big)_{xx} \\
&- \varepsilon\Delta_y\big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big) \\
= {} & \mu\Big(M \star \big(u - (1+\alpha x)\varphi^\varepsilon\big) - \big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big)\Big) \\
&- (K \star u)(x,y)u(x,y) + a(y)\big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big) \\
&- \lambda_1^\varepsilon(1+\alpha x)\varphi^\varepsilon(y) + \alpha c\varphi^\varepsilon(y) \\
= {} & \int_\Omega \big(\mu M(y,z) - u(x,y)K(y,z)\big)\Big(\big(u(x,z) - (1+\alpha x)\varphi^\varepsilon(z)\big) \\
&- \big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big)\Big)dz - u(x,y)\big(K \star (1+\alpha x)\varphi^\varepsilon\big)(y) \\
&+ \big((1+\alpha x)\varphi^\varepsilon(y) - u(x,y)\big)\int_\Omega K(y,z)dz + a(y)\big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big) \\
&- \lambda_1^\varepsilon(1+\alpha x)\varphi^\varepsilon(y) + \alpha c\varphi^\varepsilon(y) \\
> {} & \left(a(y) + \int_\Omega K(y,z)dz\right)\big(u(x,y) - (1+\alpha x)\varphi^\varepsilon(y)\big),
\end{aligned}
$$

where the last inequality holds for (x, y) in a neighbourhood of (x_0, y_0) thanks to the normalization of φ^ε:

- $u(x_0, y_0) = (1 + \alpha x_0)\varphi^\varepsilon(y_0) < \frac{\mu m_0}{k_\infty}$, which implies in particular that $\mu M(y_0, z) - u(x_0, y_0)K(y_0, z) \geq 0$ for any $z \in \Omega$,
- $\sup_{y\in\Omega} \varphi^\varepsilon(y) \leq \frac{-\lambda_1^\varepsilon}{k_\infty|\Omega|}$, which shows that

$$
\begin{aligned}
u(x_0,y_0)\big(K \star (1+\alpha x_0)\varphi^\varepsilon(y_0)\big) < u(x_0,y_0)K \star \varphi^\varepsilon &\leq -\lambda_1^\varepsilon u(x_0,y_0) \\
&= -\lambda_1^\varepsilon(1+\alpha x_0)\varphi^\varepsilon(y_0),
\end{aligned}
$$

- $c \geq 0$ and $\alpha \geq 0$.

Since (x_0, y_0) is a minimum for the function $(u(x, y) - (1 + \alpha x)\varphi^\varepsilon(y)$, Hopf's Lemma then implies that $\frac{\partial(u-(1+\alpha x)\varphi^\varepsilon)}{\partial\nu}(x_0, y_0) < 0$, which contradicts the Neumann boundary conditions satisfied by u and φ^ε. If $y_0 \in \Omega$, the same computation and the strong maximum principle lead to a contradiction. Thus $\alpha = 0$ and we have shown that $\forall x < 0$, $\varphi^\varepsilon(y) \leq u(x, y)$. In particular $\inf_{x<0,y\in\Omega} u(x, y) \geq \inf_{y\in\Omega} \varphi^\varepsilon(y) > 0$.

Step 2: We remove the dependency in ε.

Let v be a decreasing solution to (5.29) with $c = c_\varepsilon^*$ constructed in Theorem 5.5.4. Define $\tilde{v}(x, y) = v(-x, y)$. Then $\tilde{v}$ satisfies:

$$
c_\varepsilon^*\tilde{v}_x - \tilde{v}_{xx} - \varepsilon\Delta_y\tilde{v} - \mu(M \star \tilde{v} - \tilde{v}) = \tilde{v}(a(y) - K \star \tilde{v} - \beta\tilde{v}).
$$

In particular,

$$\begin{aligned}-c\tilde v_x - \tilde v_{xx} - \varepsilon\Delta_y \tilde v - \mu(M\star\tilde v - \tilde v) =&\tilde v(a(y) - K\star\tilde v - \beta\tilde v) - (c+c_\varepsilon^*)\tilde v_x\\ \leq&\tilde v(a(y) - K\star\tilde v - \beta\tilde v)\\ \leq&\tilde v(a(y) - K\star\tilde v),\end{aligned}$$

since $\tilde v_x \geq 0$. Thus $\tilde v$ is a subsolution to (5.36). Moreover, thanks to Theorem 5.5.4, $\sup v \leq \frac{\sup a}{\beta}$.

Since $\tilde v \to 0$ when $x \to -\infty$ and thanks to point 1 above, there exists $\zeta > 0$ such that $\tilde v(x+\zeta, y) \leq \frac{1}{2}\inf_{\bar x<0,\bar y\in\Omega} u(\bar x, \bar y)$ for any $(x, y) \in (-\infty, 0)\times\Omega$. We define

$$\alpha := \inf\{\zeta, \forall (x, y) \in (-\infty, 0) \times \Omega, \tilde v(x + \zeta, y) \leq u(x, y)\}.$$

Assume by contradiction that $\alpha > -\infty$. Then, there exists $x_0 < 0$, $y_0 \in \overline{\Omega}$ such that $\tilde v(x_0, y_0) = u(x_0, y_0)$ (recall that $\liminf_{x\to-\infty}\inf_{y\in\Omega} u(x, y) - \tilde v(x + \alpha, y) > 0$ by step 1). If $y \in \Omega$, then thanks to Hopf's Lemma, we have $\frac{\partial(u-\tilde v(\cdot+\alpha,\cdot))}{\partial\nu}(x_0, y_0) < 0$, which contradicts the Neumann boundary conditions satisfied by u and $\tilde v$. If $y \in \Omega$, since $u(x_0, y_0) = \tilde v(x_0, y_0) \leq \frac{\mu m_0}{k_\infty}$ and $\tilde v$ is a subsolution to equation (5.36), Lemma 5.5.5 shows that $u = \tilde v$. This is a contradiction since $\beta > 0$. Thus, for $\zeta \in \mathbb{R}$, we have $u(x, y) \geq \tilde v(x + \zeta, y)$ for any $x < 0$. Taking the limit $\zeta \to +\infty$, we get that $\inf_{x<0,y\in\Omega} u(x, y) \geq \lim_{x\to+\infty}\inf_{y\in\mathbb{R}} \tilde v(x, y) \geq \rho_\beta$, thanks to Theorem 5.5.4.

This finishes the proof of Lemma 5.5.13. □

We are now in a position to prove Theorem 5.5.10.

Proof of Theorem 5.5.10. We divide the proof in two steps.

Step 1: We construct a solution with $\limsup_{x\to+\infty}\int_\Omega u(x, y)dy = 0$.

Let (c, u) be the solution constructed in Corollary 5.5.3 with $\beta = 0$ and $\nu = \frac{1}{2}\min\left(\rho_{\beta_0}k_0|\Omega|, \frac{-\lambda_1^\varepsilon}{2}\right)$, where $\beta_0 = \frac{k_\infty \sup a}{\mu m_0}$ and ρ_{β_0} is given by Lemma 5.4.4. Assume by contradiction that $\limsup_{x\to+\infty}\int_\Omega u(x, y)dy > 0$. Then by definition there exists a real number $\kappa > 0$ and a sequence $x_n \to +\infty$ such that $\int_\Omega u(x_n, y)dy \geq \kappa$. Thanks to Lemma 5.5.12, there exists $\bar\kappa > 0$ such that $\forall n \in \mathbb{N}$, $\inf_{y\in\Omega} u(x_n, y) \geq \bar\kappa$. Let $\beta := \max\left(2\frac{\sup a}{\kappa}, \beta_0\right)$, then a direct application of Lemma 5.5.13 shows that for any $n \in \mathbb{N}$, we have $\inf_{x<x_n,y\in\Omega} u(x, y) > \rho_\beta > 0$. In particular, taking the limit $n \to \infty$, we get $\inf_{(x,y)\in\mathbb{R}\times\Omega} u(x, y) \geq \rho_\beta > 0$. Thanks to Lemma 5.5.9, this shows $\inf_{(x,y)\in\mathbb{R}\times\Omega} u(x, y) \geq \rho_{\beta_0}$. However, thanks to the normalization satisfied by u (5.24), we have

$$k_0|\Omega|\rho_{\beta_0} \leq (K\star u)(x, 0) \leq \frac{1}{2}k_0|\Omega|\rho_{\beta_0},$$

which is a contradiction. We conclude that $\limsup_{x\to+\infty}\int_\Omega u(x, y)dy = 0$.

Step 2: We show that u satisfies the other properties required by Theorem 5.5.10.

Since u is given by Corollary 5.5.3, u naturally satisfies $\int_\Omega u(x,y)dy \leq \frac{\sup a}{k_0}$.

Let us show briefly that the solution constructed in step 1 satisfies $\liminf_{x\to-\infty} \inf_{y\in\Omega} u(x,y) \geq \rho_{\beta_0}$. Indeed, thanks to Lemma 5.5.13 we have $\liminf_{x\to-\infty} \inf_{y\in\Omega} u(x,y) > 0$. Let (x_n, y_n) be a minimizing sequence with $x_n \to -\infty$. Thanks to the classical elliptic estimates, $u(x+x_n,\cdot)$ converges locally uniformly to a solution $\bar{u}$ of (5.36) with $\inf_{(x,y)\in\mathbb{R}\times\Omega} \bar{u}(x,y) > 0$. Thanks to Lemma 5.5.9 we have then $\inf_{(x,y)\in\mathbb{R}\times\Omega} \bar{u}(x,y) \geq \rho_{\beta_0}$. Finally $\liminf_{x\to-\infty} \inf_{y\in\Omega} u(x,y) = \inf_{(x,y)\in\mathbb{R}} \bar{u}(x,y) \geq \rho_{\beta_0}$.

We finally remark that Lemma 5.5.8 item (ii) gives the minimality property of the speed c_ε^*. In particular $c = c_\varepsilon^*$ for the solution (c,u) constructed here.

This ends the proof of Theorem 5.5.10. □

Next we prove an upper estimate on the limit of $\int_\Omega u(x,y)dy$ when $x \to \infty$, which is independent of ε.

Lemma 5.5.14 **($\int_\Omega u(x,y)dy \to 0$ when $x \to +\infty$).** *Let Assumption 5.2.2 hold, and suppose $\lambda_1 < 0$. There exists $\bar{\varepsilon} > 0$, $\nu > 0$ and a sequence $(x_n)_{n\in\mathbb{N}}$ independent from ε, such that if u solves (5.36) with $0 < \varepsilon \leq \bar{\varepsilon}$, $c = c_\varepsilon^*$ and satisfies $\int_\Omega u(x,z)dz \leq \nu$ for any $x \geq 0$, then*

$$\forall n \in \mathbb{N}, \forall x \geq x_n, \int_\Omega u(x,z)dz \leq \frac{\nu}{2^n}.$$

Proof. We divide the proof into three steps.

Step 1: Setting

Since $a(0) = \sup a$ and by the continuity of a, there exists $r > 0$ such that for any $|y| \leq r$, $a(y) - \mu \geq \frac{3}{4}(\sup a - \mu)$. In the rest of the proof we fix $r > 0$ such that this property holds and $B_r(y) \subset \Omega$. Notice that for $|y| \leq r$, we have $a(y) - \mu \geq \frac{3}{4}(\sup a - \mu) > 0$.

We define $\bar{\varepsilon} := \min\left(\varepsilon_0, \frac{r^2(\sup a - \mu)}{2\pi^2}\right)$, where $\varepsilon_0 > 0$ is given by Lemma 5.4.4. We let $\nu := \min\left(\frac{1}{2}\rho_{\beta_0} k_0 |\Omega|, \frac{\sup a - \mu}{4k_\infty}\right)$, where $\beta_0 = \frac{k_\infty \sup a}{\mu m_0}$ and ρ_{β_0} is given by Lemma 5.4.4. In particular, arguing as in the proof of Theorem 5.5.10, any solution u to (5.36) with $0 < \varepsilon \leq \bar{\varepsilon}$ which satisfies $\int_\Omega u(0,y)dy \leq \nu$ has limit 0 near $+\infty$, i.e. $\int_\Omega u(x,y)dy \to_{x\to+\infty} 0$.

Thanks to Lemma 5.5.12 and 5.5.13, there exists $\rho > 0$ such that if $\int_\Omega u(x,y)dy \geq \frac{\nu}{2}$, then for any $x' \leq x$ we have $\inf_{y\in\Omega} u(x,y) \geq \rho$.

We let $\alpha_0 := \max\left(\frac{\nu}{\int_{|y|\leq r} \cos\left(\frac{\pi|y|}{2r}\right)dy}, 2\rho\right)$, $\gamma := \min\left(1, \left(\frac{\sup a - \mu}{8(c_\varepsilon^*\sqrt{\alpha_0}+1)}\rho\right)^2\right)$. Notice in particular that $2c_\varepsilon^*\sqrt{\gamma}\alpha_0 + 2\gamma - \frac{\sup a - \mu}{4}\rho \leq 0$. Finally we let

$\bar{x} := \sqrt{\frac{\alpha_0}{\gamma}}$. Remark that, since $c_\varepsilon^* \to 2\sqrt{-\lambda_1} > 0$ when $\varepsilon \to 0$ (thanks to Theorem 5.3.5), $\bar{x}$ is uniformly bounded when $\varepsilon \to 0$.

Since (5.36) is invariant by translation in x we will assume w.l.o.g. that $\int_\Omega u(x,y)dy \leq \nu$ for $x \geq -\bar{x}$ instead of $x \geq 0$.

Step 2: We show that if $\int_\Omega u(x,y)dy \leq \nu$ for $x \geq -\bar{x}$ then $\int_\Omega u(\bar{x},y)dy \leq \frac{\nu}{2}$.

Here we let u be a solution to (5.36) with $0 < \varepsilon \leq \bar{\varepsilon}$, $c = c_\varepsilon^*$ and $\int_\Omega u(x,y) \leq \nu$ for $x \geq -\bar{x}$. We assume by contradiction that $\int_\Omega u(\bar{x},y)dy > \frac{\nu}{2}$. Since $u > 0$ on $(-\bar{x},\bar{x}) \times \Omega$, we define:

$$\alpha := \sup\left\{\zeta > 0, \forall x \in (-\bar{x},\bar{x}), \forall |y| \leq r, \quad (\zeta - \gamma x^2)\cos\left(\frac{\pi|y|}{2r}\right) \leq u(x,y)\right\}.$$

Assume by contradiction that $\alpha < \alpha_0$. By definition of α we have $(\alpha - \gamma x^2)\cos\left(\frac{\pi|y|}{2r}\right) \leq u(x,y)$ in $[-\bar{x},\bar{x}] \times \Omega$ and there exists $x_0 \in [-\bar{x},\bar{x}]$ and y_0 with $|y_0| \leq r$ such that $u(x_0,y_0) = (\alpha - \gamma x_0^2)\cos\left(\frac{\pi|y_0|}{2r}\right)$. Let $v := (\alpha - \gamma x^2)\cos\left(\frac{\pi|y|}{2r}\right)$. We have:

$$\begin{aligned}
0 &\leq -c_\varepsilon^*(v-u)_x(x_0,y_0) - (v-u)_{xx}(x_0,y_0) - \varepsilon\Delta_y(v-u)(x_0,y_0) \\
&= 2c_\varepsilon^*\gamma x_0 + 2\gamma + \varepsilon\left(\frac{\pi}{2r}\right)^2 v(x_0,y_0) - \mu(M \star u)(x_0,y_0) \\
&\quad - u(x_0,y_0)\big(a(y_0) - \mu - (K \star u)(x_0,y_0)\big) \\
&< 2\left(c_\varepsilon^*\sqrt{\alpha_0} + \sqrt{\gamma}\right)\sqrt{\gamma} - \frac{\sup a - \mu}{4}\rho + \left(\varepsilon\left(\frac{\pi}{2r}\right)^2 - \frac{\sup a - \mu}{4}\right)u(x_0,y_0) \\
&\leq 0,
\end{aligned}$$

since

- by definition of r, we have $a(y_0) - \mu \geq \frac{3}{4}(\sup a - \mu)$,
- $\int_\Omega u(x_0,y)dy \leq \nu$, and thus $K \star u \leq k_\infty \nu \leq \frac{\sup a - \mu}{4}$,
- $\int_\Omega u(\bar{x},y)dy \geq \frac{\nu}{2}$. Hence, since $x_0 \leq \bar{x}$, $\inf_{y\in\Omega} u(x_0,y) \geq \rho$,
- $\varepsilon \leq \bar{\varepsilon} \leq \frac{r^2(\sup a - \mu)}{2\pi^2}$,
- finally, by definition, $\gamma \leq 1$ and $\sqrt{\gamma} \leq \frac{\sup a - \mu}{8(c_\varepsilon^*\sqrt{\alpha_0}+1)}\rho$.

Hence, we have a contradiction and $\alpha \geq \alpha_0 \geq \frac{\nu}{\int_{|y|\leq r}\cos\left(\frac{\pi|y|}{2r}\right)dy}$. In particular, $(\alpha_0 - \gamma x^2)\cos\left(\frac{\pi|y|}{2r}\right) \leq u(x,y)$ and

$$\nu \leq \alpha_0 \int_{|y|\leq r} \cos\left(\frac{\pi|y|}{2r}\right) dy < \int_\Omega u(0,y)dy.$$

This contradicts our hypothesis $\int_\Omega u(x,y)dy \le \nu$ when $x \ge -\bar{x}$. We conclude that $\int_\Omega u(\bar{x},y)dy \le \frac{\nu}{2}$.

Step 3: Bootstrapping

In Step 2 we have shown that for a $\bar{x}$ which is uniformly bounded in ε, we have

$$\left(\forall x \ge -\bar{x}, \int_\Omega u(x,y)dy \le \nu\right) \Rightarrow \left(\int_\Omega u(\bar{x},y)dy \le \frac{\nu}{2}\right).$$

Since (5.36) is invariant by translation, this implication still holds for $u(x,y)$ replaced by $u(x+\delta,y)$ for any $\delta > 0$. In particular,

$$\left(\forall x \ge -\bar{x}, \int_\Omega u(x,y)dy \le \nu\right) \Rightarrow \left(\forall x \ge \bar{x}, \int_\Omega u(x,y)dy \le \frac{\nu}{2}\right).$$

Thus we can reproduce Step 1 and 2 replacing ν by $\frac{\nu}{2}$ and $u(x,y)$ by $u(x+\bar{x},y)$. We thus find by an elementary recursion a sequence of points x_n such that for $x \ge x_n$, $\int_\Omega u(x,y)dy \le \frac{\nu}{2^n}$.

This ends the proof of Lemma 5.5.14. □

5.5.4 Proof of Theorem 5.2.10

We are now in a position to let $\varepsilon \to 0$ and construct a traveling wave for equation (5.1), thus proving our main result Theorem 5.2.10.

Proof of Theorem 5.2.10. We divide the proof in three steps.

Step 1: Construction of a converging sequence to a transition kernel.

Let ε_n be a decreasing sequence with $\lim \varepsilon_n = 0$ and $\varepsilon_0 \le \bar{\varepsilon}$ (where $\bar{\varepsilon}$ is given by Lemma 5.5.14) such that for any $0 < \varepsilon \le \varepsilon_0$, $\lambda_1^\varepsilon < 0$ (such a ε_0 exists thanks to Theorem 5.3.5). Since (5.36) is invariant by translations in x, for each ε_n we can choose u^n given by Theorem 5.5.10 (with $\varepsilon = \varepsilon_n$), which satisfies moreover

$$\int_\Omega u^n(0,y)dy = \min\left(\frac{\rho_{\beta_0}}{2}, \nu\right), \qquad \forall x \ge 0, \int_\Omega u^n(x,y)dy \le \nu, \tag{5.39}$$

where ν is given by Lemma 5.5.14, $\beta_0 = \frac{k_\infty \sup a}{\mu m_0}$ and ρ_{β_0} is given by Lemma 5.4.4.

For $k \le n$, let u_k^n be the restriction of u^n to the set $[-k,k]\times\Omega$. Then $u_k^n \in M^1([-k,k]\times\overline{\Omega}) = (C_b([-k,k]\times\overline{\Omega}))^*$. Since $\int_\Omega u^n(x,y)dy \le \frac{\sup a}{k_0}$ for $x \in \mathbb{R}$, we have $\int_{-k}^k \int_\Omega u^n(x,y)dydx \le 2k\frac{\sup a}{k_0}$, and thus the sequence $(u_k^n)_{n>k}$ satisfies condition (κ.1) of Theorem 5.6.9. Moreover $[-k,k]\times\overline{\Omega}$ is compact, and thus condition (κ.2) is automatically satisfied for $(u_k^n)_{n>k}$. Thanks to Prokhorov's Theorem 5.6.9, the sequence $(u_k^n)_{n>k}$ is relatively compact in $(C_b([-k,k]\times\overline{\Omega}))^*$. Then, thanks to a classical diagonal extraction process, there exists a subsequence, still denoted u^n, and a measure $u \in M^1(\mathbb{R}\times\overline{\Omega})$ such that $u^n \rightharpoonup u$, in the sense that

$$\forall\psi \in C_c(\mathbb{R}\times\overline{\Omega}), \int_{\mathbb{R}\times\Omega} \psi(x,y)u^n(x,y)dydx \to \int_{\mathbb{R}\times\overline{\Omega}} \psi(x,y)u(dx,dy). \quad (5.40)$$

Finally, for $a<b$ and thanks to Theorem 5.6.10, we have for any Borel set $\omega \subset \overline{\Omega}$:

$$u\big((a,b)\times\omega\big) \le u\big((a,b)\times\overline{\Omega}\big) \le \liminf_{n\to\infty}\int_a^b\int_\Omega u^n(x,y)dydx \le |b-a|\frac{\sup a}{k_0}.$$

Hence, Lemma 5.6.11 applies and u is in fact a transition kernel: $u(dx,dy) = u(x,dy)dx$.

Step 2: We show that u satisfies the limit conditions (5.6) and (5.7) of Definition 5.2.9.

By construction, the function u^n satisfies $\int_\Omega u^n(0,y)dy = \min\left(\nu, \frac{\rho_{\beta_0}}{2}\right)$. Applying Lemma 5.5.12 and Lemma 5.5.13, there exists $\rho>0$ (independent from n) such that $\inf_{y\in\Omega} u^n(x,y) \ge \rho$ for any $x \le 0$. In particular, taking the limit $n\to\infty$, we have for any positive $\psi \in C_c\big((-\infty,0)\times\overline{\Omega}\big)$

$$\begin{aligned}\int_{\mathbb{R}\times\overline{\Omega}} \psi(x,y)u(x,dy)dx &= \lim_{n\to\infty}\int_{\mathbb{R}\times\Omega}\psi(x,y)u^n(x,y)dxdy \\ &\ge \rho\int_{\mathbb{R}\times\Omega}\psi(x,y)dxdy > 0,\end{aligned}$$

and then

$$\liminf_{\bar{x}\to+\infty}\int_{\mathbb{R}\times\overline{\Omega}}\psi(x+\bar{x},y)u(x,dy)dx \ge \rho\int_{\mathbb{R}\times\Omega}\psi(x,y)dxdy > 0.$$

Thus u satisfies (5.6).

Let us show that u satisfies (5.7), i.e. vanishes near $+\infty$. Thanks to Lemma 5.5.14, there exists a sequence x_k independent from n such that $\int_\Omega u^n(x,y)dy \le \frac{\nu}{2^k}$ for any $x \ge x_k$. In particular for any positive $\psi \in C_c\big((0,+\infty)\times\overline{\Omega}\big)$, we have

$$\begin{aligned}\int_{\mathbb{R}\times\overline{\Omega}} \psi(x-x_k,y)u(x,dy)dx &= \lim_{n\to\infty}\int_{\mathbb{R}\times\Omega}\psi(x-x_k,y)u^n(x,y)dxdy \\ &\le \frac{\nu}{2^k}\ \text{diam supp}\ \psi \sup_{(x,y)\in\mathbb{R}\times\Omega}\psi(x,y),\end{aligned}$$

where diam supp $\psi = \sup\left\{d\big((x,y),(x',y')\big), \psi(x,y)>0 \text{ and } \psi(x',y')>0\right\}$ is the diameter of the support of ψ. Thus

$$\limsup_{\bar{x}\to+\infty}\int_{\mathbb{R}\times\overline{\Omega}}\psi(x-\bar{x},y)u(x,dy)dx = \limsup_{k\to+\infty}\int_{\mathbb{R}\times\overline{\Omega}}\psi(x-x_k,y)u(x,dy)dx = 0,$$

and u satisfies indeed (5.7).

Let us stress that, since u satisfies (5.6) and (5.7), u is neither 0 nor a nontrivial stationary state to (5.1).

Step 3: We show that u satisfies (5.5) in the sense of distributions.

Let $F_0^y := \left\{\psi \in C_c^2(\mathbb{R}\times\overline{\Omega}), \forall x \in \mathbb{R}, \forall y \in \partial\Omega, \frac{\partial\psi}{\partial\nu}(x,y) = 0\right\}$ as in Lemma 5.6.4. We fix $\psi \in F_0^y$. Our goal here is to show that

$$\begin{aligned} & c^* \int_{\mathbb{R}\times\overline{\Omega}} \psi_x u(x,dy)dx - \int_{\mathbb{R}\times\overline{\Omega}} \psi_{xx} u(x,dy)dx \\ &= \int_{\mathbb{R}\times\overline{\Omega}} \int_{\overline{\Omega}} M(y,z)u(x,dz)\psi(x,y)dxdy + \int_{\mathbb{R}\times\overline{\Omega}} (a(y)-\mu)\psi(x,y)u(x,dy)dx \\ &\quad - \int_{\mathbb{R}\times\overline{\Omega}} \int_{\overline{\Omega}} \psi(x,y)K(y,z)u(x,dz)u(x,dy)dx, \end{aligned} \tag{5.41}$$

where $c^* = 2\sqrt{-\lambda_1}$. Multiplying (5.36) by ψ and integrating by parts, we have

$$\begin{aligned} & c_{\varepsilon_n}^* \int_{\mathbb{R}\times\Omega} \psi_x(x,y)u^n(x,y)dxdy - \int_{\mathbb{R}\times\Omega} \psi_{xx}(x,y)u^n(x,y)dxdy \\ &= \varepsilon_n \int_{\mathbb{R}\times\overline{\Omega}} \Delta_y\psi(x,y)u^n(x,y)dxdy + \int_{\mathbb{R}\times\Omega} (a(y)-\mu)\psi(x,y)u^n(x,y)dxdy \\ &\quad + \int_{\mathbb{R}\times\Omega} \psi(x,y)\int_{\Omega} M(y,z)u^n(x,z)dzdxdy \\ &\quad - \int_{\mathbb{R}\times\Omega} \psi(x,y)\int_{\Omega} K(y,z)u^n(x,y)dzu^n(x,y)dxdy. \end{aligned} \tag{5.42}$$

We are going to show convergence, up to a possible extraction, for each term in the above equation.

• Since $\psi_x(x,y)$, $\psi_{xx}(x,y)$, $\Delta_y\psi(x,y)$ and $(a(y)-\mu)\psi$ are continuous and compactly supported in $\mathbb{R}\times\overline{\Omega}$, it follows from (5.40) that

$$\begin{aligned} c_{\varepsilon_n}^* \int_{\mathbb{R}\times\overline{\Omega}} \psi_x(x,y)u^n(x,y)dxdy &\underset{n\to\infty}{\longrightarrow} c^* \int_{\mathbb{R}\times\overline{\Omega}} \psi_x(x,y)u(x,dy)dx, \\ \int_{\mathbb{R}\times\overline{\Omega}} \psi_{xx}(x,y)u^n(x,y)dxdy &\underset{n\to\infty}{\longrightarrow} \int_{\mathbb{R}\times\overline{\Omega}} \psi_{xx}(x,y)u(x,dy)dx, \\ \varepsilon_n \int_{\mathbb{R}\times\overline{\Omega}} \Delta_y\psi(x,y)u^n(x,y)dxdy &\underset{n\to\infty}{\longrightarrow} 0, \\ \int_{\mathbb{R}\times\overline{\Omega}} (a(y)-\mu)\psi(x,y)u^n(x,y)dxdy &\underset{n\to\infty}{\longrightarrow} \int_{\mathbb{R}\times\overline{\Omega}} (a(y)-\mu)\psi(x,y)u(x,dy)dx, \end{aligned}$$

since $c_\varepsilon^* = 2\sqrt{-\lambda_1^\varepsilon} \underset{\varepsilon\to 0}{\to} 2\sqrt{-\lambda_1} = c^*$.

• Next, the function $y \mapsto \int_{\mathbb{R}\times\Omega} \psi(x,y)M(y,z)u^n(x,z)dz$ converges uniformly to $y \mapsto \int_{\mathbb{R}\times\overline{\Omega}} \psi(x,y)M(y,z)u(x,dz)dx$ thanks to [186, Appendix, Lemma 1]. Thus

$$\int_{\mathbb{R}\times\overline{\Omega}} \psi(x,y)(M\star u^n)(x,y)dxdy \underset{n\to\infty}{\longrightarrow} \int_{\mathbb{R}\times\overline{\Omega}} \psi(x,y)\int_{\overline{\Omega}} M(y,z)u(x,dz)dxdy.$$

• The convergence of the nonlinear term requires more work. For $i\in\mathbb{N}$, let $K^i(y,z)\in F_0^2$ be such that $\|K-K^i\|_{C_b(\overline{\Omega}\times\overline{\Omega})}\leq \frac{1}{i}$ and $\|K^i\|_{C^\alpha(\overline{\Omega}\times\overline{\Omega})}\leq C$, where F_0^2 is the set of smooth kernels with null boundary flux in z, and C is independent from i (see Lemma 5.6.4 item (*iii*)). We want to complete, up to extractions, the informal diagram

$$\begin{array}{ccc} v_i^n(x,y) := \int_\Omega K^i(y,z)u^n(x,z)dz & \underset{n\to+\infty}{\overset{?}{\longrightarrow}} & v_i(x,y) := \int_{\overline{\Omega}} K^i(y,z)u(x,z)dz \\ \downarrow{\scriptstyle i\to\infty} & & \downarrow{\scriptstyle i\to\infty} \\ v^n(x,y) := \int_\Omega K(y,z)u^n(x,z)dz & \underset{n\to+\infty}{\overset{?}{\longrightarrow}} & v(x,y) := \int_{\overline{\Omega}} K(y,z)u(x,z)dz. \end{array}$$

We first show that $v_i^n(x,y)\to v_i(x,y)$ when $n\to\infty$ in $C_b\big([-R,R]\times\overline{\Omega}\big)$ for arbitrary $R>0$. We fix R so that supp $\psi\subset[-R,R]\times\overline{\Omega}$. Substituting z to y, multiplying equation (5.36) by K^i and integrating in z, we have

$$-c^*_{\varepsilon_n}(v_i^n)_x-(v_i^n)_{xx}=R^n(x,y)$$

where $R^n(x,y)$ is bounded in L^∞ uniformly in n:

$$\begin{aligned} |R^n(x,y)| &= \left|\varepsilon_n\int_\Omega \Delta_z K^i(y,z)u^n(x,z)dz+\mu\int_\Omega K^i(y,z)(M\star u^n)(x,z)dz\right. \\ &\quad \left.+\int_\Omega K^i(y,z)(a(z)-\mu-K\star u^n)u^n(x,z)dz\right| \\ &\leq \varepsilon_n\|K^i\|_{C_b(\overline{\Omega},C^2(\overline{\Omega}))}\frac{\sup a}{k_0}+\mu m_\infty|\Omega|\frac{\sup a}{k_0}\|K^i\|_{C_b(\overline{\Omega}\times\overline{\Omega})} \\ &\quad +\left(\sup a+\mu+k_\infty\frac{\sup a}{k_0}\right)\frac{\sup a}{k_0}\|K^i\|_{C_b(\overline{\Omega}\times\overline{\Omega})}. \end{aligned}$$

For n large enough so that $\varepsilon_n\leq\frac{1}{\|K^i\|_{C_b(\overline{\Omega},C^2(\overline{\Omega}))}}$, thanks to [108, Theorem 9.11] and the classical Sobolev imbeddings, $\|v_i^n(\cdot,y)\|_{C^\alpha([-R,R])}$ is uniformly bounded by a constant independent from n, i and $y\in\overline{\Omega}$. Since $K^i\in C^\alpha(\overline{\Omega}\times\overline{\Omega})$ uniformly in i, v_i^n is then uniformly Hölder in x and y and we have $\|v_i^n\|_{C^\alpha([-R,R]\times\overline{\Omega})}\leq C_R$ with C_R independent from n and i. In particular, there exists an extraction $\varphi^i(n)$ such that

– $\|v_i^{\varphi^i(n)}\|_{C^\alpha([-R,R]\times\overline{\Omega})}\leq C_R$, and

– $\|v_i^{\varphi^i(n)}-\tilde{v}_i\|_{C_b([-R,R]\times\overline{\Omega})}\to_{n\to\infty} 0$, for a function $\tilde{v}_i(x,z) \in C^\alpha\big([-R,R]\times\overline{\Omega}\big)$. Notice that we can assume w.l.o.g. that $\varphi^i(n)$ is extracted from $\varphi^{i-1}(n)$. Finally, for any test function $\xi(x) \in C_c\big([-R,R]\big)$, we have

$$\int_{-R}^{R} \xi(x) v_i^{\varphi^i(n)}(x,y)dx = \int_{-R}^{R}\int_\Omega \xi(x)K^i(y,z)u^{\varphi^i(n)}(x,z)dzdx$$
$$\to_{n\to\infty} \int_{-R}^{R}\int_{\overline{\Omega}} \xi(x)K^i(y,z)u(x,dz)dx = \int_{-R}^{R}\xi(x)v_i(x,z)dx,$$

since u^n converges to u in the sense of measures. This shows that $\tilde{v}^i(x,y) = v_i(x,y)$ for almost every $x\in[-R,R]$.

Moreover since $\|v_i\|_{C^\alpha([-R,R]\times\overline{\Omega})} \leq C_R$, there exists an extraction ζ such that $v_{\zeta(i)}$ converges in $C_b\big([-R,R]\times\overline{\Omega}\big)$ to $v(x,y) = \int_{\overline{\Omega}} K(y,z)u(x,dy)$, which shows a regularity on v.

Thanks to a diagonal extraction process, we can then construct an extraction $\varphi(n)$ such that

– $\|v_{\zeta(n)}^{\varphi(n)} - v_{\zeta(n)}\|_{C_b([-R,R]\times\overline{\Omega})} \to_{n\to\infty} 0$, and

– $\|v_{\zeta(n)} - v\|_{C_b([-R,R]\times\overline{\Omega})} \to_{n\to\infty} 0$.

Along this subsequence, we have then:

$$\left|\int_\Omega K(y,z)u^{\varphi(n)}(x,y)dxdy - \int_{\overline{\Omega}} K(y,z)u(x,dy)\right|$$
$$\leq \left|\int_\Omega \big(K(y,z)-K^{\zeta(n)}(y,z)\big)u^{\varphi(n)}(x,y)dxdy\right| + \left\|v_{\zeta(n)}^{\varphi(n)} - v_{\zeta(n)}\right\|_{C_b([-R,R]\times\overline{\Omega})}$$
$$+ \|v_{\zeta(n)} - v\|_{C_b([-R,R]\times\overline{\Omega})}$$
$$\leq \|K-K^{\zeta(n)}\|_{C_b(\overline{\Omega}\times\overline{\Omega})}\frac{\sup a}{k_0} + o_{n\to\infty}(1)$$

which shows that $\int_\Omega K(y,z)u^{\varphi(n)}(x,y)dxdy \to \int_{\overline{\Omega}} K(y,z)u(x,dy)$ in the space $C_b([-R,R]\times\overline{\Omega})$.

We are now in a position to handle the nonlinear term, by the convergence of the previously constructed subsequence. We write

$$\begin{aligned}
&\int_{\mathbb{R}\times\Omega\times\Omega} \psi(x,y)K(y,z)u^{\varphi(n)}(x,z)u^{\varphi(n)}(x,y)dxdydz \\
&= \int_{\mathbb{R}\times\Omega} \psi(x,y) \int_{\overline{\Omega}} K(y,z)u(x,dz)u^{\varphi(n)}(x,y)dxdy \\
&\quad + \int_{\mathbb{R}\times\Omega} \psi(x,y)\Big(\int_{\Omega} K(y,z)u^{\varphi(n)}(x,z)dz - \int_{\overline{\Omega}} K(y,z)u(x,dz)\Big) \\
&\quad \times u^{\varphi(n)}(x,y)dxdy \\
&= \int_{\mathbb{R}\times\Omega} \psi(x,y) \int_{\overline{\Omega}} K(y,z)u(x,dz)u^{\varphi(n)}(x,y)dxdy \\
&\quad + O\left(\|v^{\varphi(n)}(x,y) - v(x,y)\|_{C_b([-R,R]\times\overline{\Omega})}\right),
\end{aligned}$$

where, as above, $v^{\varphi(n)}(x,y) = \int_\Omega K(y,z)u^{\varphi(n)}(x,z)dz$ and v is defined by $v(x,y) = \int_{\overline{\Omega}} K(y,z)u(x,dz)$. Since $\psi(x,y)\int_{\overline{\Omega}} K(y,z)u(x,dz)$ is a continuous, compactly supported function, we have shown that

$$\begin{aligned}
&\int_{\mathbb{R}\times\Omega\times\Omega} \psi(x,y)K(y,z)u^{\varphi(n)}(x,z)u^{\varphi(n)}(x,y)dxdydz \\
&\qquad\qquad \to_{n\to\infty} \int_{\mathbb{R}\times\overline{\Omega}\times\overline{\Omega}} \psi(x,y)K(y,z)u(x,dz)u(x,dy)dx.
\end{aligned}$$

• Thus we can take the limit in (5.42) along the subsequence $\varphi(n)$. This shows that u satisfies (5.5) in a weak sense, where the test functions are taken in F_0^y. Since F_0^y is dense in $C_c^2\big(\mathbb{R}, C_b(\overline{\Omega})\big)$, equation (5.41) holds for test functions ψ taken in $C_c^2(\mathbb{R}, C_b(\overline{\Omega}))$. In particular, u satisfies (5.5) in the sense of distributions.

This ends the proof of Theorem 5.2.10. □

5.6 Appendix

5.6.1 On the principal eigenvalue

The results we recall here are established in [60, 61, 62] in a context slightly different from ours. However, in each case the proofs adapts easily to our situation and we will thus omit them.

For $b \in C_b(\overline{\Omega})$, let us define the *principal eigenvalue* of the operator $M+b$ by

$$\lambda_p(\mathcal{M}_\Omega+b) := \sup\{\lambda, \exists\varphi\in C_b(\overline{\Omega}), \varphi>0 \quad \text{s.t. } M\star\varphi+(b+\lambda)\varphi \le 0\}, \tag{5.43}$$

and recall the result of [60].

Theorem 5.6.1 (Various dependencies)**.** *1. Assume $\Omega_1 \subset \Omega_2$, then for $b \in C_b(\Omega_2)$,*

$$\lambda_p(\mathcal{M}_{\Omega_1} + b) \geq \lambda_p(\mathcal{M}_{\Omega_2} + b).$$

2. Fix Ω and assume $b_1(y) \geq b_2(y)$, then

$$\lambda_p(\mathcal{M}_{\Omega} + b_2) \geq \lambda_p(\mathcal{M}_{\Omega} + b_1).$$

3. Fix Ω. Then $\lambda_p(\mathcal{M}_\Omega + b)$ is Lipschitz continuous in b. More precisely,

$$|\lambda_p(\mathcal{M}_\Omega + b_1) - \lambda_p(\mathcal{M}_\Omega + b_2)| \leq \|b_2 - b_1\|_{L^\infty(\Omega)}.$$

In the case where $\frac{1}{\sup b - b} \notin L^1(\Omega)$, Coville [60] proved the existence of a continuous positive eigenfunction associated with λ_p for convolution-like kernels. As stated in [61], the result holds for general kernels in bounded domains:

Theorem 5.6.2 (No concentration)**.** *Assume $\frac{1}{\sup b - b} \notin L^1_{loc}(\overline{\Omega})$. Then there exists a positive continuous eigenfunction φ associated with $\lambda_p = \lambda_p(\mathcal{M}_\Omega + b)$, which solves*

$$M \star \varphi + (b(y) + \lambda_p)\varphi = 0.$$

Later, Coville, Dávila and Martínez [62] gave the following characterization of λ_p when M is a convolution kernel:

Theorem 5.6.3 (On continuous eigenfunctions)**.** *There exists a continuous eigenfunction associated with λ_p if and only if $\lambda_p < -\sup b$.*

5.6.2 Density of the space of functions with null boundary flux

Here we prove elementary results that are crucial to our proofs of Theorem 5.3.5, Theorem 5.2.6 and Theorem 5.2.10.

Lemma 5.6.4 (Density of spaces of functions with null boundary flux)**.** *Let $\Omega \subset \mathbb{R}^n$ be a bounded open set with C^3 boundary.*

(i) The function space

$$F_0 := \left\{ \psi \in C^2(\overline{\Omega}), \forall y \in \partial\Omega, \frac{\partial \psi}{\partial \nu}(y) = 0 \right\}$$

is dense in $C_b(\overline{\Omega})$.

(ii) The function space

$$F_0^y := \left\{ \psi \in C_c^2(\mathbb{R} \times \overline{\Omega}), \forall x \in \mathbb{R}, \forall y \in \partial\Omega, \frac{\partial \psi}{\partial \nu}(x, y) = 0 \right\}$$

is dense in $C_c^2(\mathbb{R}, C_b(\overline{\Omega}))$.

(iii) The function space

$$F_0^2 := \left\{ \psi \in C^2(\overline{\Omega} \times \overline{\Omega}), \forall (y,z) \in \overline{\Omega} \times \partial\Omega, \frac{\partial \psi}{\partial \nu_z}(y,z) = 0 \right\}$$

is dense in $C_b(\overline{\Omega} \times \overline{\Omega})$. *Moreover for any* $\alpha \in (0,1)$ *and* $\psi \in C^2(\overline{\Omega} \times \overline{\Omega})$ *there exists a constant* C *and a sequence* $\psi^r \to \psi$ *such that we have* $\|\psi^r\|_{C^\alpha(\overline{\Omega} \times \overline{\Omega})} \leq C \|\psi\|_{C^\alpha(\overline{\Omega} \times \overline{\Omega})}$.

Proof. Let us denote $d(y)$ the distance function

$$d(y) := \inf_{z \in \partial\Omega} |y - z|.$$

We recall that, thanks to [91], there exists $R > 0$ such that $y \mapsto d(y, \partial\Omega)$ is C^3 in the tubular neighbourhood $\Omega_R := \{y \in \Omega, d(y, \partial\Omega) < R\}$. We fix a smooth function $\theta : \mathbb{R} \to \mathbb{R}$ such that

- $\theta(x) = 0$ for $x \leq 0$,
- $\theta(1) = 1$ for $x \geq 1$, and
- $\forall k > 0$, $\theta^{(k)}(0) = \theta^{(k)}(1) = 0$.

Finally for $y \in \Omega$, we let $P(y)$ be the projection of y on $\partial\Omega$, which is well-defined and C^2 on Ω_R.

Step 1: We prove item (i).

For $\psi \in C^2(\overline{\Omega})$ and $0 < r < R$, we define

$$\psi^r(y) := \left(1 - \theta\left(\frac{d(y)}{r}\right)\right) \psi(P(y)) + \theta\left(\frac{d(y)}{r}\right) \psi(y).$$

Then $\psi^r \in C^2(\overline{\Omega})$. Moreover,

$$\|\psi^r - \psi\|_{C_b(\Omega)} \leq \sup_{d(y,\partial\Omega) \leq r} \left|\psi\big(P(y)\big) - \psi(y)\right|.$$

Since $\overline{\Omega}$ is compact, ψ is uniformly continuous on $\overline{\Omega}$ and the right-hand size is thus arbitrarily small. Finally for $y \in \partial\Omega$,

$$\begin{aligned}
\frac{\partial \psi^r}{\partial \nu}(y) = \nabla \psi^r(y) \cdot \nu &= \big(1 - \theta(0)\big)\Big(D_y P \nabla \psi\big(P(y)\big)\Big) \cdot \nu \\
&\quad - \frac{\theta'(0)}{r} \psi\big(P(y)\big) \nabla d(y) \cdot \nu \\
&\quad + \frac{\theta'(0)}{r} \psi(y) \nabla d(y) \cdot \nu + \theta(0) \nabla \psi(y) \cdot \nu \\
&= 0,
\end{aligned}$$

since $Im(D_y P) \subset \nu^\perp$ and $\theta(0) = 0$, $\theta'(0) = 0$. This shows item (i).

Step 2: We prove item (*ii*).
Let $\psi \in C_c^2(\mathbb{R} \times \overline{\Omega})$. We define for $0 < r < R$

$$\psi^r(x,y) := \left(1 - \theta\left(\frac{d(y)}{r}\right)\right)\psi\big(x, P(y)\big) + \theta\left(\frac{d(y)}{r}\right)\psi(x,y).$$

As before, $\psi^r \in C_c^2(\mathbb{R} \times \overline{\Omega})$, and for each $x \in \mathbb{R}$, $y \in \partial\Omega$, we have $\frac{\partial \psi^r}{\partial \nu}(x,y) = 0$. Moreover,

$$\begin{aligned}\|\psi^r - \psi\|_{C_c^2(\mathbb{R}, C_b(\overline{\Omega}))} = &\sup_{(x,y)\in\mathbb{R}\times\overline{\Omega}} \max\big(|\psi^r(x,y) - \psi(x,y)|,\\ &|\psi^r_x(x,y) - \psi_x(x,y)|, |\psi^r_{xx}(x,y) - \psi_{xx}(x,y)|\big)\\ \leq &\, \|\psi(x,P(y)) - \psi(x,y)\|_{C_c^2(\mathbb{R}, C_b(\Omega_r))},\end{aligned}$$

where the right-hand side can be chosen arbitrarily small. This shows item (*ii*).

Step 3: We prove item (*iii*).
Let $\psi \in C_c^2(\overline{\Omega} \times \overline{\Omega})$. We define for $0 < r < \frac{R}{2}$

$$\psi^r(y,z) := \left(1 - \theta\left(\frac{d(z)}{r}\right)\right)\psi\big(y, P(z)\big) + \theta\left(\frac{d(z)}{r}\right)\psi(y,z).$$

As before, $\psi^r \in C_c^2(\overline{\Omega} \times \overline{\Omega})$, and for each $y \in \overline{\Omega}$, $z \in \partial\Omega$, we have $\frac{\partial \psi^r}{\partial \nu_z}(y,z) = 0$. Clearly, $\psi^r \to \psi$ in $C_b(\Omega)$. Moreover, for each $(y,z) \in \overline{\Omega} \times \overline{\Omega}$ we have $(\psi^r - \psi)(y,z) = \left(1 - \theta\left(\frac{d(z)}{r}\right)\right)\big(\psi(y,P(z)) - \psi(y,z)\big)$ and thus

$$\begin{aligned}&\frac{\Big|\big(\psi^r(y,z) - \psi(y,z)\big) - \big(\psi^r(y,z') - \psi(y,z')\big)\Big|}{|z - z'|^\alpha}\\ &\leq \frac{\left|\theta\left(\frac{d(z)}{r}\right) - \theta\left(\frac{d(z')}{r}\right)\right|}{|z - z'|^\alpha}\big(\psi(y,P(z)) - \psi(y,z)\big)\\ &\quad + \left|1 - \theta\left(\frac{d(z')}{r}\right)\right|\left(\frac{|\psi(y,P(z)) - \psi(y,P(z'))|}{|z - z'|^\alpha} + \frac{|\psi(y,z) - \psi(y,z')|}{|z - z'|^\alpha}\right)\\ &\leq \|\theta\|_{C^\alpha([0,1])}\|d\|^\alpha_{C^{0,1}(\Omega_{\frac{R}{2}})}\|\psi\|_{C^\alpha(\overline{\Omega}\times\overline{\Omega})} + 2\|\psi\|_{C^\alpha(\overline{\Omega}\times\overline{\Omega})}.\end{aligned}$$

This shows item (*iii*). □

5.6.3 Topological theorems

For the sake of completeness, we present here two results from [212] we use in our work, namely the Leray-Schauder fixed point 5.6.5 — corresponding to [212, Corollary 13.1 item (iii)]— and the global continuation principle 5.6.6 — found in [212, Theorem 14 C].

Theorem 5.6.5 (Leray-Schauder fixed point theorem)**.** *Let G be an open bounded subset of a Banach space X and $T:\overline{G}\to X$ be a compact operator. Assume that $0\in G$ and for all $(t,x)\in(0,1]\times\partial G$,*

$$tTx \neq x.$$

Then $ind(T,G)=1$, where ind is the Leray-Schauder fixed point index.

Theorem 5.6.6 (Global continuation principle of Leray-Schauder (1934))**.** *Let X be a Banach space and $H:[\mu_1,\mu_2]\times\overline{G}\to X$ be compact, where G is an bounded open set.*

Assume

1. *There exists no solution of $H(\mu,x)=x$ in $[\mu_1,\mu_2]\times\partial G$, and*
2. *$ind(H(\mu_1,\cdot),G)\neq 0$.*

Then, there exists a compact connected set C of solutions to $H(\mu,x)=x$ which connects the set $\{\mu_1\}\times G$ to the set $\{\mu_2\}\times G$.

Let us recall a result that we proved in a joint work with M. Alfaro [7], and that we use in the construction of stationary states. We first recall the classical Krein-Rutman theorem.

Theorem 5.6.7 (Krein-Rutman theorem)**.** *Let E be a Banach space. Let $C\subset E$ be a closed convex cone of vertex 0, such that $C\cap -C=\{0\}$ and $Int\, C\neq\varnothing$. Let $T:E\to E$ be a linear compact operator such that $T(C\backslash\{0\})\subset Int\, C$.*

Then, there exists $u\in Int\, C$ and $\lambda_1>0$ such that $Tu=\lambda_1 u$. Moreover, if $Tv=\mu v$ for some $v\in C\backslash\{0\}$, then $\mu=\lambda_1$. Finally, we have

$$\lambda_1=\max\{|\mu|,\mu\in\sigma(T)\},$$

and the algebraic and geometric multiplicity of λ_1 are both equal to 1.

We now state the result from [7]:

Theorem 5.6.8 (Bifurcation under Krein-Rutman assumption)**.** *Let E be a Banach space. Let $C\subset E$ be a closed convex cone with nonempty interior $Int\, C\neq\varnothing$ and of vertex 0, i.e. such that $C\cap -C=\{0\}$. Let*

$$\begin{array}{rccc} F: & \mathbb{R}\times E & \to & E \\ & (\alpha,x) & \mapsto & F(\alpha,x) \end{array}$$

be a continuous and compact operator, i.e. F maps bounded sets into relatively compact ones. Let us define

$$\mathcal{S}:=\overline{\{(\alpha,x)\in\mathbb{R}\times E\backslash\{0\}:F(\alpha,x)=x\}}$$

the closure of the set of nontrivial fixed points of F, and

$$\mathbb{P}_{\mathbb{R}}\mathcal{S} := \{\alpha \in \mathbb{R} : \exists x \in C\backslash\{0\}, (\alpha, x) \in \mathcal{S}\}$$

the set of nontrivial solutions in C.

Let us assume the following.

1. *$\forall \alpha \in \mathbb{R}$, $F(\alpha, 0) = 0$.*

2. *F is Fréchet differentiable near $\mathbb{R} \times \{0\}$ with derivative αT locally uniformly w.r.t. α, i.e. for any $\alpha_1 < \alpha_2$ and $\epsilon > 0$ there exists $\delta > 0$ such that*

$$\forall \alpha \in (\alpha_1, \alpha_2),\ \|x\| \leq \delta \Rightarrow \|F(\alpha, x) - \alpha T x\| \leq \epsilon \|x\|.$$

3. *T satisfies the hypotheses of Theorem 5.6.7 (Krein-Rutman), i.e. $T(C\backslash\{0\}) \subset \operatorname{Int} C$. We denote by $\lambda_1(T) > 0$ its principal eigenvalue.*

4. *$\mathcal{S} \cap (\{\alpha\} \times C)$ is bounded locally uniformly w.r.t. $\alpha \in \mathbb{R}$.*

5. *There is no fixed point on the boundary of C, i.e. $\mathcal{S} \cap (\mathbb{R} \times (\partial C\backslash\{0\})) = \varnothing$.*

Then, either $\left(-\infty, \frac{1}{\lambda_1(T)}\right) \subset \mathbb{P}_{\mathbb{R}}\mathcal{S}$ or $\left(\frac{1}{\lambda_1(T)}, +\infty\right) \subset \mathbb{P}_{\mathbb{R}}\mathcal{S}$.

The proof can be found in [7].

5.6.4 Measure theory

Let us recall here Prokhorov's Theorem, which plays a key role in this article. Our version is adapted from the original paper [171, Theorem 1.12]; for the sake of completeness, let us give two other references, the book of Schwartz [186, Appendix, Theorem 3], and the book of Bogachev, [36, Theorem 8.6.2].

Theorem 5.6.9 (Prokhorov's Theorem)**.** *Let X be a complete separable metric space. A subset $\mathfrak{M} \subset (C_b(X))^*$ is relatively compact for the weak-* topology if, and only if,*

(κ.1) the set $\{\mu(X), \mu \in \mathfrak{M}\} \subset \mathbb{R}$ is bounded, and

(κ.2) for any $\varepsilon > 0$, there exists a compact set $K_\varepsilon \subset\subset X$ such that, for all $\mu \in \mathfrak{M}$,

$$\mu(X\backslash K_\varepsilon) \leq \varepsilon.$$

Next we present some properties of the weak convergence of measures. The result is adapted from [36, Theorem 8.2.3 and Corollary 8.2.4].

Theorem 5.6.10 (Properties of the weak convergence)**.** *Let X be a complete separable metric space, and $\mu_n, \mu \in (C_b(X))^*$. The following conditions are equivalent:*

(i) μ_n *converges weakly to* μ*, i.e. for any* $\psi \in C_b(X)$*, we have* $\lim \int_X \psi(x)\mu_n(dx) \to \int_X \psi(x)\mu(dx)$*,*

(ii) $\lim \mu_n(X) = \mu(X)$ *and for any open set* $G \subset X$*,* $\liminf \mu_n(G) \geq \mu(G)$*,*

(iii) $\lim \mu_n(X) = \mu(X)$ *and for any closed set* $F \subset X$*,* $\limsup \mu_n(F) \leq \mu(F)$*.*

Next we show a disintegration lemma with *ad hoc* hypotheses.

Lemma 5.6.11 (Disintegration)**.** *Let* Ω *be an open domain* $\Omega \subset \mathbb{R}^d$*, and let* μ *be a nonnegative measure defined on* $\mathcal{B}(\mathbb{R} \times \overline{\Omega})$*. Assume there exists a constant* $C \geq 0$ *such that*

$$\forall a < b, \forall \omega \in \mathcal{B}(\overline{\Omega}), \mu([a, b] \times \omega) \leq C|b - a|.$$

Then there exists a function $\nu : \mathbb{R} \times \mathcal{B}(\overline{\Omega}) \longrightarrow \mathbb{R}^+$ *such that*

1. *for almost every* $x \in \mathbb{R}$*,* $\omega \mapsto \nu(x, \omega)$ *is a nonnegative finite measure on* $\mathcal{B}(\overline{\Omega})$
2. *for every* $\omega \in \mathcal{B}(\overline{\Omega})$*,* $x \mapsto \nu(x, \omega)$ *is a Lebesgue-measurable function in* $L^1_{loc}(\mathbb{R})$

and:

$$\mu(dx, dy) = \nu(x, dy)dx$$

in the sense that

$$\forall \varphi \in C_c(\mathbb{R} \times \overline{\Omega}), \int_{\mathbb{R}\times\overline{\Omega}} \varphi(x, y)\mu(dx, dy) = \int_{\mathbb{R}\times\overline{\Omega}} \varphi(x, y)\nu(x, dy)dx$$

where $C_c(\mathbb{R} \times \overline{\Omega})$ *is the set of continuous functions on* $\mathbb{R} \times \overline{\Omega}$ *with compact support.*

Finally ν *is unique up to a Lebesgue neglectable set, and satisfies*

$$\nu(x, \overline{\Omega}) \leq C \qquad a.e.$$

Proof. We divide the proof in four steps.

Step 1: We construct a density for $\mu(A \times \omega)$, $\omega \in \mathcal{B}(\overline{\Omega})$.

Let us take $\omega \in \mathcal{B}(\overline{\Omega})$, and define $A \in \mathcal{B}(\mathbb{R}) \overset{\mu_\omega}{\mapsto} \mu(A \times \omega)$. Then μ_ω is a nonnegative Borel-regular measure on $\mathcal{B}(\mathbb{R})$. Indeed μ_ω is clearly well-defined on $\mathcal{B}(\mathbb{R})$, satisfies the σ-additivity property and is finite on any compact set. Then, for any open set $U \subset \mathbb{R}$, we have

$$\mu_\omega(U) \leq C\mathcal{L}(U).$$

Indeed we can write $U = \bigcup_{n\in\mathbb{N}} K_n$ where K_n is an increasing sequence of compact sets of the form $K_n = \bigsqcup_{i=0}^{m_n} [a_i^n, b_i^n]$ (with $a_i^n < b_i^n < a_{i+1}^n ...$), for which the property holds by assumption. Thus

$$\mu_\omega(U) = \lim_{n\to+\infty} \mu_\omega(K_n) \leq C \lim_{n\to+\infty} \mathcal{L}(K_n) = C\mathcal{L}(U)$$

Finally, $\mu_\omega \ll \mathcal{L}$, where $\mathcal{L}$ is the Lebesgue measure on $\mathbb{R}$. Indeed, let us take $E \subset \mathbb{R}$ bounded such that $\mathcal{L}(E) = 0$. Then by the regularity of μ_ω [184, Theorem 2.18], we have

$$\mu_\omega(E) = \inf_{U \text{ open}, U\supset E} \mu_\omega(U) \leq C \inf_{U \text{ open}, U\supset E} \mathcal{L}(E) = 0.$$

Thanks to the Radon-Nikodym Theorem [184, Theorem 6.10], there exists then a unique measurable function $h_\omega \in L^1_{loc}(\mathbb{R})$ such that

$$\mu_\omega = h_\omega \mathcal{L} = h_\omega dx.$$

Step 2: We show that the density h_ω is well-defined up to a neglectable set independant from ω.

Let ω_n be an enumeration of the sets of the form

$$\overline{\Omega} \cap \prod_{i=1}^{d} [a_i, b_i]$$

where $a_i, b_i \in \mathbb{Q}$. Clearly, ω_n is stable by finite intersections, and the associated monotone class is $\mathcal{B}(\overline{\Omega})$. We let $h_n := h_{\omega_n} \in L^1_{loc}(\mathbb{R})$ be the previouly constructed density associated with μ_{ω_n}. Then h_n is well-defined on a set $\mathcal{D}_n$ satisfying $\mathcal{L}(\mathbb{R}\backslash\mathcal{D}_n) = 0$. We let $\mathcal{D} = \bigcap_{n\in\mathbb{N}} \mathcal{D}_n$, then $\mathcal{L}(\mathbb{R}\backslash\mathcal{D}) = 0$ and by construction, every h_n is well-defined on $\mathcal{D}$.

We take $\omega \in \mathcal{B}(\overline{\Omega})$ and show that, up to a redefinition on a neglectable set, the function h_ω is well-defined on $\mathcal{D}$. If ω is open, then we can write

$$\omega = \bigsqcup_{n\in\mathbb{N}} \omega'_n$$

for a well-chosen extraction ω'_n of ω_n. Thus for any $A \in \mathcal{B}(\mathbb{R})$, we have

$$\mu_\omega(A) = \mu(A \times \omega) = \sum_{n\in\mathbb{N}} \mu(A \times \omega'_n)$$

hence by the uniqueness in the Radon-Nikodym Theorem, we have:

$$h_\omega = \sum_{n\in\mathbb{N}} h_{\omega'_n} \qquad \mathcal{L} - a.e.$$

Since $\sum h_{\omega'_n}$ is a measurable function on $\mathcal{D}$, we can take the above equality as our definition of h_ω. In the general case, using the Borel regularity of μ, we write for $A \in \mathcal{B}(\mathbb{R})$:

$$\mu(A \times \omega) = \inf_{U \text{ open}, U \supset \omega} \mu(A \times U),$$

which shows that h_ω is well-defined on $\mathcal{D}$.

Step 3: We verify that the constructed family of functions form a nonnegative measure on $\overline{\Omega}$ for $\mathcal{L}$-a.e. $x \in \mathbb{R}$.

Let $w_n \in \mathcal{B}(\overline{\Omega})$ be a countable collection of Borel sets with $w_i \cap w_j = \varnothing$ if $i \neq j$. Then

$$\mu(A \times \bigsqcup_{n \in \mathbb{N}} w_n) = \sum_{n \in \mathbb{N}} \mu(A \times w_n)$$

for any $A \in \mathcal{B}(\mathbb{R})$, and thanks to the uniqueness in the Radon-Nikodym theorem we have

$$h_{\bigsqcup_{n \in \mathbb{N}} w_n} = \sum_{n \in \mathbb{N}} h_{w_n} \qquad \mathcal{L} - a.e.$$

Thus, for any $x \in \mathcal{D}$, the function $\omega \mapsto h_\omega(x)$ is σ-additive. Since h_ω is nonnegative by construction, then $\omega \mapsto h_\omega(x)$ is a nonneagtive measure on $\mathcal{B}(\overline{\Omega})$.

We define $\nu(x, \omega) := h_\omega(x)$. Then ν matches the definition of a transition kernel (Definition 5.2.1).

Step 4: Conclusion.

Since $\nu(x, dy)dx$ coincides with μ on the monotone class $A \times \omega_n$, where $A \in \mathcal{B}(\mathbb{R})$, we have $\mu(dx, dy) = \nu(x, dy)dx$ on $\mathcal{B}(\mathbb{R} \times \overline{\Omega})$.

Finally, since $x \mapsto \nu(x, \overline{\Omega})$ is in $L^1_{loc}(\mathbb{R})$, then almost every point of $\nu(x, \overline{\Omega})$ is a Lebesgue point (thanks to [184, Theorem 7.7]) and thus:

$$\nu(x_0, \overline{\Omega}) = \lim_{r \to 0} \frac{1}{2r} \int_{x_0 - r}^{x_0 + r} \nu(x_0 + s, \overline{\Omega}) ds \leq \frac{1}{2r}(2rC) = C$$

for $\mathcal{L}$-a.e. $x_0 \in \mathbb{R}$.

This finishes the proof of Lemma 5.6.11 $\square$

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Résumé

Cette thèse porte sur différents modèles de propagation en épidémiologie évolutive. L'objectif est d'en faire une analyse mathématique rigoureuse puis d'en tirer des enseignements biologiques. Dans un premier temps nous envisageons le cas d'une population d'hôtes répartis de manière homogène dans un espace linéaire, dans laquelle se propage un pathogène pouvant muter entre deux phénotypes plus ou moins virulents. Ce phénomène de mutation est à l'origine d'une interaction entre les dynamiques évolutive et épidémiologique du pathogène. Nous étudions la vitesse de propagation de l'épidémie et l'existence de fronts progressifs, ainsi que l'influence sur la vitesse de différents facteurs biologiques, comme des effets stochastiques liés à la taille de la population d'hôtes (explorations numériques). Dans un deuxième temps nous envisageons une hétérogénéité spatiale périodique dans la population d'hôtes, et l'existence de fronts pulsatoires pour le système de réaction-diffusion (non-coopératif) associé. Enfin nous considérons un pathogène pouvant muter vers un grand nombre de phénotypes différents et étudions l'existence de fronts potentiellement singuliers, modélisant ainsi une concentration sur un trait optimal.

Mots clefs : épidémiologie évolutive, vitesse de propagation, équations de réaction-diffusion (non-locales), fronts progressifs, fronts pulsatoires, concentration.

Summary

In this thesis we consider several models of propagation arising in evolutionary epidemiology. We aim at performing a rigorous mathematical analysis leading to new biological insights. At first we investigate the spread of an epidemic in a population of homogeneously distributed hosts on a straight line. An underlying mutation process can shift the virulence of the pathogen between two values, causing an interaction between epidemiology and evolution. We study the propagation speed of the epidemic and the influence of some biologically relevant quantities, like the effects of stochasticity caused by the hosts' finite population size (numerical explorations), on this speed. In a second part we take into account a periodic heterogeneity in the hosts' population and study the propagation speed and the existence of pulsating fronts for the associated (non-cooperative) reaction-diffusion system. Finally, we consider a model in which the pathogen is allowed to shift between a large number of different phenotypes, and construct possibly singular traveling waves for the associated nonlocal equation, thus modelling concentration on an optimal trait.

Keywords: evolutionary epidemiology, propagation speed, traveling waves, (non-local) reaction-diffusion equations, pulsating fronts, concentration.